

SOCIAL BIOLOGY OF THE NEOTROPICAL WASP
*MISCHOCYTTARUS DREWSENI*¹

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ABSTRACT

The biology of the social wasp *Mischocyttarus drewseni* (Hymenoptera, Vespidae) is described from the Lower Amazon region of Brazil. The study is based on direct observation of marked adults and on daily records of brood development of 53 colonies under natural conditions.

M. drewseni inhabits areas of low vegetation and prefers to nest under eaves of buildings, in sheds and barns, and in other protected sites. The nest is a single, uncovered, round comb of hexagonal paper cells, suspended horizontally from a long, narrow stem. Nesting material consists of woody plant fibers chewed up and mixed with small amounts of salivary secretion that hardens into a tough, chitinlike material. The nest stem is built up almost entirely of this secretion.

Adults and larvae both feed on arthropod prey and on plant nectar and honeydew. Workers find prey by sight, pouncing from flight on any irregularity in the outline of a stem or twig. Nectar is collected from floral and extra-floral sources. When nectar is abundant it is stored in the form of droplets on the walls of cells containing eggs. Larvae produce a clear salivary secretion that is eaten by adults.

M. drewseni protects its brood from certain predaceous ants by chemical means. At the base of the terminal sternite is a gland whose product is secreted onto a tuft of hair. Females apply this secretion by rubbing the tuft against the nest stem, where it is effective in keeping scout ants from gaining access to the nest and discovering the brood. Dominance encounters between females on the nest resemble those described for *Polistes* in that there exists a linear hierarchy, at the top of which is the egg-laying queen; the hierarchy results in a trophic advantage to higher-ranking females. It differs from *Polistes* in that subordinate females are involved in dominance interactions primarily during the first two weeks of adult life. Degree of participation in dominance interactions is apparently closely related to the state of ovarian development.

There is a division of labor between queens and workers. Queens are at the top of the dominance hierarchy, are the primary egg-layers, prepare cells to receive eggs, initiate construction of most cells, and forage primarily for pulp. Workers are subordinate to queens, heighten cell walls, forage for pulp and food, distribute food to nest-mates and larvae, and bring water to the nest for cooling.

New colonies are founded by offspring of declining colonies; this may occur at any time of the year. Most colonies are founded by single females, though up to eight sibling females may associate to found a colony. The first three or four offspring develop rapidly; subsequent larvae

take much longer to develop. As workers emerge and begin to help the foundress care for brood, the larval development time gradually decreases again. At the time the first pupae appear the first unfertilized eggs are laid, these giving rise to the first adult males six weeks later. At about the time males appear, nonworking females also begin to appear on the nest. For the next ten weeks or so males and nonworking females emerge at a high rate, while the number of workers emerging gradually diminishes. There are no morphological differences between workers, queens, and nonworkers, though workers tend to be somewhat smaller.

Evidence is presented to support the hypothesis that decline and termination of colony development is dependent primarily upon changes in the ratio of males and nonworkers to workers, and not upon the reproductive condition of the queen.

In the typical colony the founding female does not remain as queen for the entire life of the colony, but is superseded by an offspring who succeeds in out-dominating her and forcibly ejecting her from the nest. The new queen is in turn eventually ousted by a younger nestmate. The average life span of four colonies was 160 days, while the average egg-laying life of five queens was only 49 days.

The average life span (total time on the nest as adult) of queens was 61 days, of workers 31 days, of nonworkers 5.0 days, and of males 4.8 days. Survivorship curves are given for workers, nonworkers, and males. Though the total number of adults produced by a colony may approach 200, because of the relatively short life span of adults, there are rarely more than 30 adults in a colony at any one time.

I. INTRODUCTION

Mischocyttarus is the largest genus of social wasps, surpassing even *Polistes* in number of species described (186). Yet, unlike the cosmopolitan genus *Polistes*, *Mischocyttarus* has achieved its extraordinary diversity wholly within the New World, where it is one of 20 genera in the vespidae subfamily Polistinae. With the exception of *Polistes*, which is the only one of these whose range brings it into the backyards of naturalists the world over, all of these genera are tropical and for this reason have remained little studied. The presumed tropical origin of the social Vespidae (Richards and Richards, 1951; van der Vecht, 1966) and the rich diversity

of genera and species in the tropics are strong arguments for carrying the study of vespidae biology into these regions. This paper reports the first detailed study of the social biology of tropical *Mischocyttarus*.

Most of what is known about the biology of *Mischocyttarus* is scattered through a relatively small literature (H. von Ihering, 1896; Ducke, 1907, 1914; Williams, 1928; Bequaert, 1933; Rau, 1933; Vesey-Fitzgerald, 1938; Snelling, 1953). O. W. Richards revised the genus in 1945 and included extensive biological notes. Zikán's revision (1949) contains fragmentary biological observations. In two other papers (1935, 1951) Zikán records biological observations on *Mischocyttarus*.

Mischocyttarus invited study for several reasons. First, the morphological distinctiveness of the genus suggested that there exists specialized behavior not found in other genera. Second, the remarkable diversity of nest structure within the genus suggested an equal diversity of behavioral adaptations. Third, the large number of species hinted at a successful adaptive radiation, possibly based on specialized behavior. Finally, its small colonies and open nest structure facilitated detailed observations of all activities of adults on the nest at all times. I decided to conduct the study in the equatorial tropics for two reasons. First, it seemed appropriate to study the genus close to the center of its distribution, where it presumably evolved. Second, I was interested in choosing an area with minimal seasonal fluctuations of climate in hopes of exposing the intrinsic factors that regulate colony cycle. *M. drewseni* was selected because it was the most abundant species in the study region.

The present study has as its primary aim to provide an account of the details of the social organization and life cycle of *Mischocyttarus drewseni*, based on direct observation of the activities of marked adult wasps and on records of colony development. It is hoped that it will provide a basis for future comparative studies

within the genus, as well as for comparison with other genera. The most significant new findings presented are: 1) discovery of the means by which *M. drewseni* protects its brood against destruction from ants; 2) the relation of age of adults to their involvement in dominance interactions; 3) survivorship statistics for workers, nonworkers, and males; 4) relationship between duration of the larval stage and stage of colony development; and 5) the details of colony development, with a tentative interpretation of the factors regulating it.

II. MATERIALS AND METHODS

A. TAXONOMY AND DISTRIBUTION

The most recent revision of the hymenopteran superfamily Vespoidea is that of Richards (1962). He divided the group into three families: Masaridae, Eumenidae, and Vespidae. Within the Vespidae, which comprise the groups that have achieved sociality, Richards has included three subfamilies: Stenogastrinae, Vespinae, and Polistinae. The Stenogastrinae comprise three genera occurring in the Oriental and Australian regions. The three vespine genera are primarily of the north temperate regions. The Polistinae contain 25 genera, most of them tropical in distribution, though *Polistes* is cosmopolitan. The subfamily Polistinae is divided into three tribes: Ropalidiini, Polybiini, and Polistini. The Polybiini comprise 22 genera, 19 of them, including *Mischocyttarus*, limited to the New World.

The genus *Mischocyttarus* is separated from other Polybiini primarily on the basis of the asymmetrical tarsal lobes of the adults. The larvae are also distinct from those of other genera in that they possess one, two, or three lobes on the ventral side of the first abdominal segment, and an enlarged first thoracic spiracle (Reid, 1942).

The genus has been revised by Richards (1945) and by Zikán (1949); Willink (1953)

revised the Argentinian species. Zikán (1949) states that the 165 species in his revision, when added to the species in Richards' list, bring the total number of species in the genus to 225, but in fact many of those in Zikán's key are also present in that of Richards. By my count, there are 183 different species in the two revisions. Add to these the three new species described by Willink, and the total number of described species reaches 186.

The genus ranges from southwestern Canada and southeastern United States to northern Argentina, with the greatest number of species occurring in the tropics. *Mischocyttarus drewseni* has been recorded from Surinam, Guyana, Venezuela, Colombia, Peru, Brazil, Paraguay, and Argentina. Five varieties and races have been described. The species is a medium-sized wasp, 15–18 mm long, dark-brown to black in color. Its body is slender, and the first abdominal segment is elongated.

B. LOCATIONS OF THE STUDY

The data for this study were gathered in the field in the Lower Amazon region of Brazil. Field observations on *M. drewseni* were made at two localities: Belém, Pará (1°27'S, 48°29'W), on the southern shore of the bay of Guajará and 120 km from the sea, and Fazenda Taperinha, on the Rio Ayayá (a *paraná*, or lateral channel, of the main Amazon stream), approximately 40 km east of Santarém, Pará (2°26'S, 45°41'W). Both localities are well within the limits of the Amazonian rainforest, or "Hylaea." Altitudes at both localities are less than 30 meters.

Although Belém averages 27 percent more precipitation per year, both localities experience approximately the same monthly distribution of rainfall. January through June are the wettest months, July through December the driest. The average monthly temperature fluctuates within less than 1°C (26.3–26.8°C) at Belém and within less than 2°C (25.7–27.4°C) at Taperinha. Thus, by far the most notice-

TABLE 1. Average monthly rainfall (in mm.) for Belém and Taperinha, Pará, Brazil (Reed, 1941, p. 474-5).

Month	Belém	Taperinha
January	193	165
February	148	171
March	170	170
April	200	163
May	141	151
June	111	160
July	156	111
August	110	110
September	80	98
October	81	126
November	68	110
December	106	119
Year	1,700	1,600

TABLE 2. Average monthly temperature (in degrees Fahrenheit) for Belém and Taperinha, Pará, Brazil (Reed, 1941, p. 474-5).

Month	Belém	Taperinha
January	86.3	86.3
February	86.3	86.3
March	86.3	86.3
April	86.3	86.3
May	86.3	86.3
June	86.3	86.3
July	86.3	86.3
August	86.3	86.3
September	86.3	86.3
October	86.3	86.3
November	86.3	86.3
December	86.3	86.3

able seasonal change at both localities is amount of rainfall. Rainfall and temperature data for both localities are summarized in Tables 1 and 2. Since both localities are near the equator, day length varies but little from 12 hours throughout the year.

C. PERIOD OF THE STUDY

The field study lasted from 20 August 1967 to 31 May 1969. Most of the period from 20 August 1967 through 15 May 1968 was spent in Belém. Continuous observations were made at Taperinha from 15 May 1968 until 8 May 1969, with the exception of the period from 1 August to 14 October 1968. Other interruptions of continual observations were necessary but were minor.

D. METHODS OF STUDY

This study is based primarily on 520 hours of direct observation of colonies of *Mischocyttarus drewseni** *in situ*. Data were taken from 53 colonies of *M. drewseni*, 19 at Belém and 34 at Taperinha.

The adults of 20 of the colonies of *M. drewseni* at Taperinha were marked for individual identification. When a colony was first discovered, the usual procedure was to anaesthetize the entire adult population with ether. Ether was preferred to CO₂ because of its availability and ease of administration. According to W. E. Kerr (personal communication), ether has less effect on subsequent behavior of stingless

* Determination confirmed by O. W. Richards, Imperial College, London.

bees than does CO₂. As each new adult emerged it was carefully removed from the nest with forceps, etherized, and marked.

Adults were marked on the thorax with Testor's "Pla" model airplane dope. This was found to be satisfactory, though it was necessary to keep the dope at the right consistency by the use of linseed oil as a thinner. The dope thickened with repeated opening of the bottles. Spots applied with dope that was too thick tended to flake off. If the dope was too thin, the spots tended to spread over the surface of the mesonotum and into the articulations of the tegulae, hindering flight. When this happened, it was necessary to remove the paint with fine forceps after it had dried and re-mark the individual. Such manipulations did not affect the wasps in any visible way.

Colonies of *M. drewseni* were numbered consecutively. Adults were identified as members of a given colony with a combination of two of five colors, one spot on either side of the midline of the scutellum. All adults within a colony were numbered consecutively in order of emergence by the use of a code of five colors in five positions on the mesonotum. (The only exceptions to consecutive numbering were numbers 20, 30, and 40 of colony 174, which were marked after number 10 and before number 11.) Marking in this way caused no apparent ill effects, nor did it hinder normal movements of the wasps.

Adult behavior was observed at all times of the day. Notes were recorded on tape in the field and transcribed at the end of each day. For some colonies adult activities were timed with a stopwatch.

At the end of each observation day each nest was checked for brood development. For ease of tabulation of these data the cells of each nest were numbered. The first cell constructed was number "1," then, as new cells were added to this, they were numbered in a spiral manner. This spiral numbering system was found to be the best way of approximating the order in which

cells were added. In nests discovered later in their development it was sometimes not possible to be sure which was the original cell. In such cases a central cell was arbitrarily denoted "1." The content of each cell was recorded as either "empty," "egg," "larva," or "pupa." Larvae were divided into "small," "medium," and "large," though the criterion was relative size and was not based on instars. For purposes of the study a "larva" became a "pupa" when it had spun its silken cocoon, closing the cell. Newly constructed cells were recorded.

Rates of egg eating and abortion were obtained from these data and supplemented by direct observation. A larva replaced by an egg or empty cell was assumed aborted. An egg replaced by an empty cell was assumed eaten. Pupae disappearing in significantly less than the average time of development were assumed aborted.

The following designation of colony stages is followed:

Pre-emergence stage: from nest initiation to emergence of the first adult offspring.

1) *Egg substage*: from nest initiation to eclosion of the first larva.

2) *Larval substage*: from eclosion of the first larva to the spinning of the first cocoon.

3) *Pupal substage*: from the spinning of the first cocoon to emergence of the first adult.

Postemergence stage: from emergence of the first adult through decline.

1) *Pre-male substage*: from emergence of first adult to emergence of first male.

2) *Postmale substage*: from emergence of the first male to beginning of decline.

3) *Decline*: from beginning of irreversible reduction of brood population through final abandoning of the nest.

This classification is preferred to Yoshikawa's (1962) division of the cycle into "solitary," "superindividual," "social," and three "hibernant" stages. The term "solitary" is both inaccurate, since several females may associate to found a colony,

and misleading, for it suggests an affinity with the life cycle of solitary species, a relation that may or may not exist. The hibernant stages are irrelevant to tropical life cycles, since daughter colonies are founded immediately upon the disintegration of parent colonies.

I have followed Eberhard's (1969) classification of females:

Queen: the primary egg-layer.

Worker: a female that foraged for insects or pulp during its recorded stay on a nest.

Nonworker: a female that did not forage. For purposes of calculating caste ratios, females that subsequently became workers were classed as nonworkers during their first three days as adults, since they did no work during this period of "maturation."

The following terminology is used in referring to females on multiple-foundress nests:

Co-foundress: any one of the females associating to form a multiple-foundress colony. Co-foundresses include the *queen* and her *subordinates*.

Photographs were made with a 35 mm camera using a 135 mm lens extended with a bellows. Electronic ring-flash provided illumination. Motion pictures were used in the analysis of certain movements.

III. THE COLONY CYCLE—A BRIEF OUTLINE

Colonies of *M. drewseni* are founded by a single female working alone, or by several females in association. As soon as the first cell is built an egg is laid in it. Cells are added at a rate of about one a day, each receiving an egg as it is built, until the first eggs hatch. Nest growth stops and does not begin again until the first larvae spin cocoons and pupate. After the first adult offspring emerge the rate of growth (in terms of cells initiated) increases slightly. The first 15 or so offspring are all females, most of which develop worker behavior and assist on the

nest. After this males and nonworking females as well as workers emerge. The nest continues to grow in size, and the proportion of males and nonworkers increases relative to the total adult population for three to four months. Around this time the rate of nest growth decreases to zero, the incidence of abortion of larvae and pupae rises, increasing numbers of cells are left empty, and the adult population diminishes until the nest is empty of brood and abandoned. The entire cycle requires approximately six months.

The colony cycle will be discussed in greater detail below (The Colony Cycle, p. 118).

IV. HABITAT AND NEST SITE

According to Ducke (1905) *Mischocyttarus drewseni* inhabits fields and open places. My own experience corroborates this finding. The colonies in Belém were in a swampy area of tall grass with isolated clumps of small trees (Plate I, fig. 1). The nests at Taperinha were in a clearing on "terra firma" along the edge of the Rio Ayayá (Plate I, fig. 2). This area was grazed by cattle, goats, and horses from approximately March through July. The vegetation consisted of low grass with scattered trees and clumps of shrubs 1–3 m tall. All foraging activities of the adult wasps were confined to these areas of low vegetation. I have never seen either nests or foragers of *M. drewseni* in forest of any kind.

Five days of searching the rather small (about ten acres) clearing in the Ducke Forest Reserve, 26 km north of Manaus in the state of Amazonas, turned up no nests of *M. drewseni*. It may be that this area was cleared so recently (about five years before) and remained so isolated (surrounded by several km of rainforest) that the habitat had not yet been colonized by the species. The same was true at Curuá, a logging camp about 60 km east of Santarém. Although the clearings and areas

TABLE 3. Nesting situations and substrates of *M. drewseni*.

	Nest	Situation	Approximate height above ground (m)	Substrate	Direction of exposure
Belém	180	window lintel	5	bare wood	south
	180a	" "	"	" "	"
	180b	" "	"	" "	"
	181	" "	"	" "	west
	182	" "	"	" "	"
	183	ceaves	5	" "	north
	184	window lintel	2.5	" "	south
	194	" "	5	" "	north
	195	ceaves	6	" "	west
	195a	window lintel	5	" "	"
	195b	" "	"	" "	"
	195c	" "	"	" "	"
	195d	" "	"	" "	"
	195e	" "	"	" "	south
	195f	" "	"	" "	north
	195g	ceaves	6	" "	"
	195h	"	"	" "	"
	195i	window lintel	5	" "	south
	195j	ceaves	6	" "	west
Taperinha	163	"	5	" "	southeast
	165	under sill beam of gallery	1.5	" "	west
	166	" " " " "	"	" "	"
	167	" " " " "	"	" "	"
	168	" " " " "	"	" "	"
	169	" " " " "	"	" "	"
	173	ceaves	2	" "	south
	174	"	"	" "	east
	175	"	1.5	" "	"
	223	"	"	" "	north

of young second-growth vegetation were quite extensive, and although I spent nine days of intensive searching there, I turned up only one colony of *M. oecothrix*, a forest-dwelling species (Richards, 1945). Again, the habitat was less than five years old and was very isolated from similar habitats.

Table 3 gives nesting situation and substrate for each of the 53 nests of *M. drewseni* found. All but one of the nests were built on man-made structures. Of these, 46 (88 percent) were attached to unpainted wood. Painted wood was

avoided; often a spot from which paint had peeled was chosen in preference to surrounding painted surfaces. Plate II, figs. 3 and 4 show nesting sites at Taperinha.

Nest 349 was the only nest that was constructed on a natural substrate. It was attached to the midrib on the underside of a leaf in the center of a low clump of dense shrubbery (Plate I, fig. 2). Unfortunately, the nest was destroyed, probably by passing cattle, a few days after it was initiated. Had the nest grown to maturity its weight would undoubtedly

TABLE 3 (continued). Nesting situations and substrates of *M. drowseni*.

Nest	Situation	Approximate height above ground (m)	Substrate	Direction of exposure
230	inside open barn	3.5	steel roofing	west
231	" " "	"	" "	"
237	eaves	1.5	bare wood	south
258	stack of roofing tiles	0.3	ceramic tile	west
264	fence rail	0.6	bare wood	"
268	eaves	1.5	" "	north
295	stack of fence rails	3.15	" "	west
310	inside open barn	1.5	steel roofing	east
342	under sill beam of gallery	2.5	bare wood	west
347	eaves	2	" "	south
349	under leaf in dense bush	0.3	leaf midrib	all sides
353	inside open barn	4	steel roofing	west
354	under sill beam of gallery	2.5	bare wood	"
380	chicken coop	1	" "	east, west
388	eaves	3	" "	east
389	"	"	" "	"
421	"	"	" "	south
422	stack of roofing tiles	0.3	ceramic tile	"
423	eaves	1.5	bare wood	east
430	chicken coop	1	" "	east, west
432	eaves	2	" "	north
436	"	"	" "	east
437	"	"	" "	"
493	chicken coop	1	" "	east, west

have caused the leaf to hang vertically. I suspect, therefore, that *M. drowseni* does not normally choose leaves of this size as nest sites. *Polistes canadensis*, which builds nests of a size similar to that of *M. drowseni*, also builds on man-made structures if available, but in the wild chooses the undersides of large limbs, hollows in trees, and the undersides of palm fronds and spathes. *M. drowseni* probably also utilizes such sites in the wild.

Twenty-three of the nests had a west-facing exposure, while only eight were open to the north, twelve to the south, and ten to the east. These differences are significant at the 1 percent level (Chi Square). The apparent preference for west-facing

exposure may be real; prevailing winds are from the east, with occasional storms from both the northeast and the southeast. On the other hand, it may merely reflect an unequal distribution of suitable nest sites among the four directions. The data are too few and the requirements for nest site too poorly understood to distinguish between these alternative conclusions.

None of the nests studied was so exposed as to be rained upon in a storm. Only one nest was obviously affected by weather: nest 347 was destroyed when the roofing board from which it was suspended was torn away in a high wind.

Height above the ground varied considerably (Table 3) and seemed to be

secondary to securing suitable protection from the weather.

V. NEST CONSTRUCTION

A. NEST ARCHITECTURE AND SIZE

The nest of *Mischocyttarus drewseni* consists of a single, discoid comb suspended from its center by a narrow stem (Plate III, fig. 5). The comb consists of hexagonal cells which open on its underside, or face (Plate III, fig. 6). There is no envelope surrounding the nest. The average diameter of completed cells was 4.75 mm (range: 4.40–4.95 mm) (measured between midpoints of opposite walls). There was no difference in size of cells that produced workers, nonworkers and males; indeed, the same cell in a nest sometimes produced all three castes in three different generations of brood. The average thickness of cell walls was 0.28 mm (range: 0.23–0.31 mm). Eight mature nests averaged 14 cells in diameter (range: 11–20). The nest stems of 21 nests averaged 19 mm in length (range: 12–31 mm). The stems of mature nests were 1–2 mm in diameter.

B. NEST MATERIAL

The nest of *M. drewseni* is constructed of woody plant fibers. The origins of 37 loads of pulp were observed. Of these, 18 (49 percent) were taken from the bare wood of planks, fence rails, and posts. Fifteen loads (40 percent) were collected from the dried cortex of the living or dead stems of *Stachytarpheta cayennensis* (Verbenaceae), a low, herbaceous plant. Also utilized was the dried bark of dead trees (3 loads of 37 = 8 percent), and the dried stem of an unidentified herbaceous vine (1 load in 37 = 3 percent).

C. FORAGING FOR NEST MATERIAL

A forager going after nest material often first imbibed water (7 times in 15 trips). Foragers landed on grass and other low plants near the nest, then crawled down

along a stem until they reached a deep leaf axil which contained a drop of water from the last rain. Or they went to puddles of standing water, where they landed on low plants or grass, then crawled down a stem until the surface of the water was reached. Finally, foragers obtained water from wet mud. This water, presumably stored in the crop, was carried to the source of nest material, where it was regurgitated gradually onto the surface as the nest material was collected.

The primary function of the water is probably to cause the fibers to adhere to one another as they are collected into a ball. It may also serve as a vehicle for the small amount of nest construction secretion that is apparently mixed with the fibers to make them adhere to one another on the nest (Richards and Richards, 1951). The water may also serve to soften the fibers to facilitate their removal from the substrate. It is possible that a crop full of water suffices for two or more loads of material, and for this reason a forager need not stop for water prior to each collection. For instance, in one case a forager made two trips for nest material without stopping for water, but on the third trip she did. Regardless of whether or not water was first imbibed, the ball of pulp collected was always moist enough to stick together.

The plant fibers are removed from the substrate with the mandibles. The wasp works with the grain and works backward, collecting the loosened fibers into a wet ball of pulp held behind the mandibles. The material is collected into an amorphous mass, not in a continuous strip as in *Polistes canadensis* (Eberhard, 1969, and personal observation), even though the sources used by the two species may be identical. If suitable material is scattered over the surface, as is often the case with the cortex of living *Stachytarpheta* stems, the wasp may have to move from place to place along the stem in order to find enough. In four to seven minutes the wasp collects a ball approaching the size of her

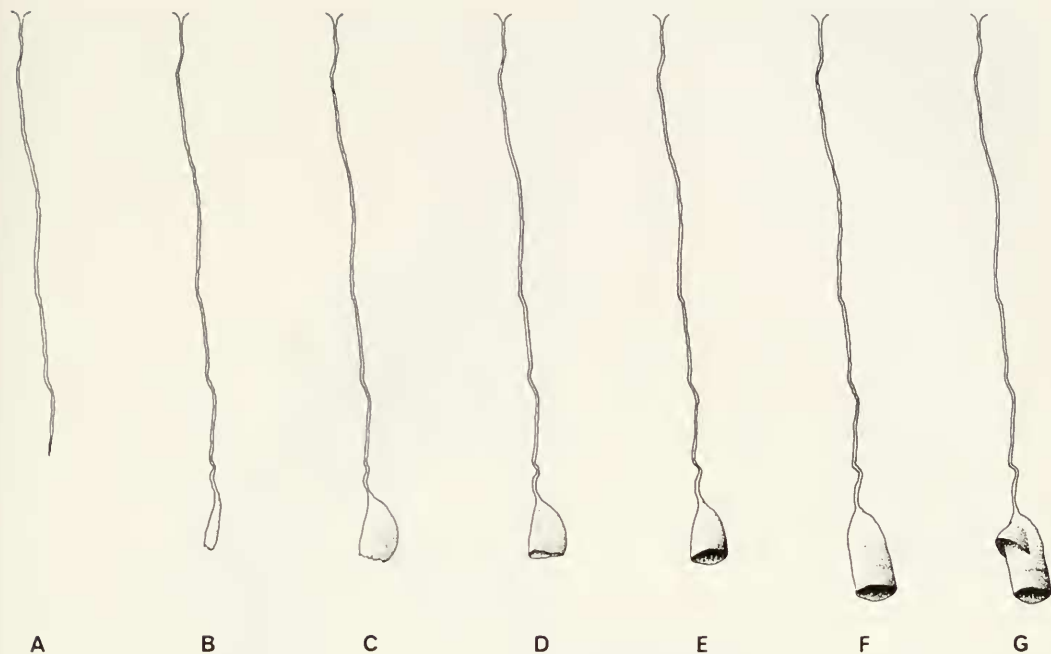


Figure 1. Stages in the initiation of a nest of *M. drewseni*. One day and seven loads of pulp were required for the single foundress to progress from stage A to G.

head (2–4 mm). She adjusts it briefly in her mandibles, using her forelegs to maneuver it, then returns to the nest. As far as it was possible to determine, the forelegs are not used to aid in holding the load during carriage.

At the nest the load of pulp may either be shared with one or more others on the nest, including the queen, or the forager may apply it to the nest herself (see Division of Labor, p. 91). In any case there is little further mastication of the pulp. The fibers are thus apparently merely removed from the substrate, moistened and mixed with a small amount of nest construction material and applied to the nest. The particles of material are coarse and chip-like.

A given forager frequently returned repeatedly over a period of hours or days to the same source for nest material. In one such case the same forager returned four times in succession over the course of

90 minutes to the same dead *Stachytarpheta* plant. Further evidence of this was frequently seen in the nest itself. One nest was constructed entirely of pulp of four discrete colors: black, gray, dark brown, and light brown. Observation revealed that each of the four workers was responsible for one of the colors, suggesting that each had its own private source of material to which it returned repeatedly.

D. NEST INITIATION

Figure 1A–G shows successive stages in early nest construction (nest 347). By the end of the first day the single foundress had succeeded in constructing the nest stem (Fig. 1A). This consisted of an extremely thin (0.2–0.3 mm) filament of pulp mixed with a large amount of a secretion produced by a gland that opens in the oral cavity. I call this material the “nest construction secretion.” The thoracic portion of the labial gland has been reported to be

the source of the building cement in *Vespa* (Janet, 1903). At 17:30 a final load of pulp was added to the lower end of the stem and was flayed out into a flat expansion (Fig. 1B). At 09:30 on the following day the wasp added the next load, using it to broaden the expansion (Fig. 1C). At 10:30 she added the next load, this time thickening the lower end of the expansion (Fig. 1D). At 11:00 the third load of the day was used to fashion a shallow cup, the base of the first cell (Fig. 1E). The next loads were used to heighten the walls of this first cell (Fig. 1F). By 14:30 this cell contained an egg and a second cell had been started (Fig. 1G). By 10:00 the following morning a third cell had been initiated, and by noon the second cell contained an egg and a fourth cell had been constructed.

E. CELL INITIATION

The second cell of a newly founded nest may be placed on any side of the cylindrical first cell. Subsequent cells, however, always straddle the groove between two adjacent cells. The first load of pulp is used to form a crescent-shaped ridge across the groove at the upper end of the cells. This is then expanded into a half of a hemisphere to form the floor of the cell. An egg is usually laid in the new cell by about this stage.

F. CELL HEIGHTENING

As the larvae grow the walls of their cells are heightened by the workers to keep pace. A worker with pulp moves over the face of the nest, rapidly inspecting the cells with her antennae, until she finds one in need of heightening. This is apparently judged by the length of the larva relative to the length of its cell, and not on the basis of the length of the cell relative to adjacent cells, since a cell containing an isolated large larva may be heightened several millimeters beyond the walls of surrounding cells.

Often when a worker moves about the

nest with a load of pulp the larvae become active, stretching their bodies so that they project beyond the rims of their cells. Some movement accompanies this stretching behavior. Larvae never respond in this way to the movements of a worker with a lump of solid food. Perhaps this response on the part of the larvae informs the worker with pulp as to which larval cells are most in need of heightening.

The load of pulp is usually applied in its entirety during the first pass or two, leaving a thick, lumpy rim to the cell. Then it is worked with the mandibles for several minutes until a uniformly thin wall is achieved. Occasionally only part of a load is used on a single cell and the rest applied elsewhere.

The walls between adjacent cells are straight, resulting in the hexagonal shape of cells surrounded on all sides. A worker heightening a cell uses one antenna inside each of the two cells sharing the wall she is heightening, in the manner Eberhard (1969) described for *Polistes*. Apparently by sensing the far walls of these cells, the antennae act as guides to keep the new work straight and centered.

Once a cell has produced an adult and received a new egg, the adults chew the walls down, reducing them somewhat in height, and apply the resulting bit of material elsewhere on the nest.

The wasps construct the entire nest using a single technique, namely the shaping of pulp into walls of a uniform thickness. Unlike certain other vespid genera, *Mischocyttarus* does not spread pulp in a thin layer over a surface.

G. ADDITION OF PULP TO CAPS OF PUPAL COCOONS

When a larva is ready to pupate it spins a silken cocoon in the upper end of its cell, closing the opening of the cell and sealing itself inside. Within a few hours after this, the workers apply pulp in a series of low ridges to the surface of this cap, effectively covering it with pulp (Plate III, fig. 6).

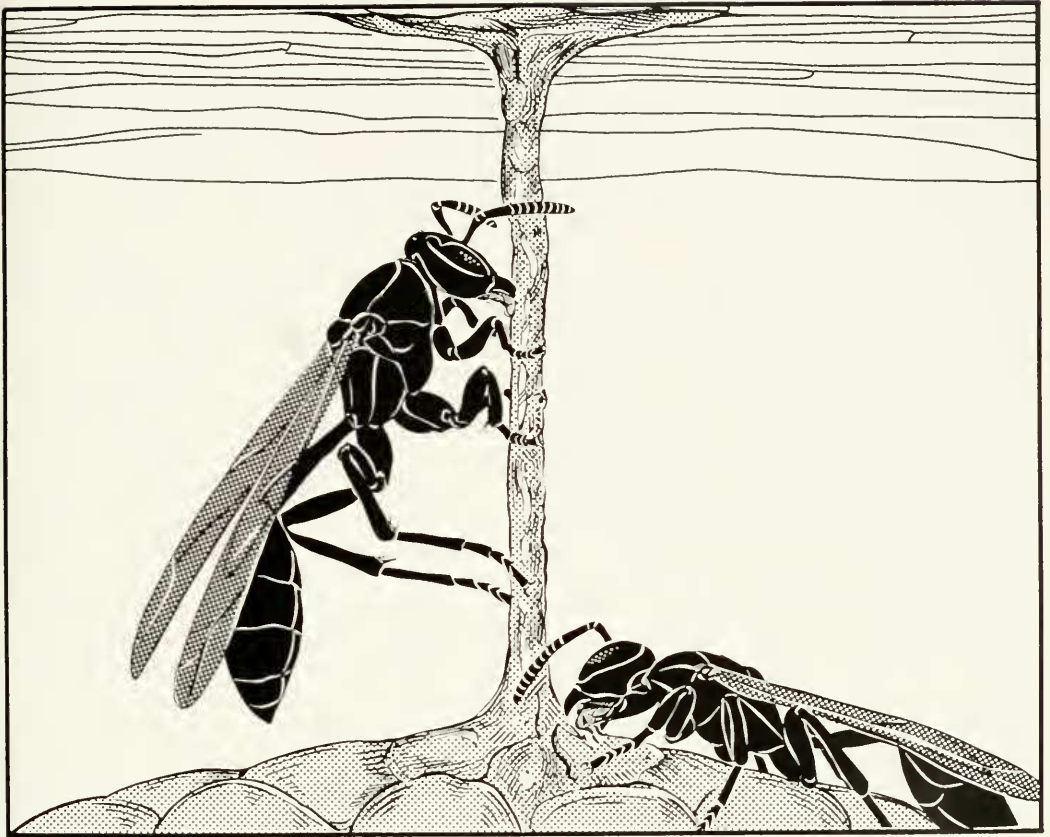


Figure 2. Mouthing: application of nest construction secretion. The wasp on the left is applying secretion to the nest stem itself, and the wasp on the right is mouthing the point of attachment of the stem to the comb. In this manner the nest support is strengthened as the nest grows and gains in weight.

This is also practiced by *M. lecointei*, *M. collarellus*, and, according to Vesey-Fitzgerald (1938), by *M. surinamensis*. This has at least two effects: 1) it serves to stiffen the delicate silk cap, making it less susceptible to damage as the adults move about over the nest face, and 2) it serves to camouflage the bright white of the silk, making the nest a more uniform color and less conspicuous from below.

Certain other species of *Mischocyttarus* (e.g., *M. injucundus* and *M. fitzgeraldi*) do not do this, but apparently apply the nest construction secretion to the caps. This has the same two effects as the application of pulp.

II. MOUTHING

As the nest increases in size the nest stem is continually thickened by repeated applications of the nest construction secretion. A wasp climbs the nest stem and "mouths" the base of attachment, using a licking movement of her mouthparts, then she slowly works her way backward down the stem until the top of the nest is reached (Fig. 2). This is repeated for up to 30 minutes at a time. The secretion hardens into a tough, plasticlike material. The stem from a large nest, when cut transversely, is seen to consist of many extremely thin concentric layers of this material surrounding the original pulp core. These layers can

be peeled off in small sheets of extremely thin pliable film.

The material is also applied in lesser amounts to the entire nest surface, gradually decreasing in thickness from the point of attachment of the stem to the periphery of the comb. One or a few layers are applied to the outer walls of all cells, right down to their rims.

The material no doubt serves primarily to lend strength and rigidity to the nest structure. The stem of a large nest is extremely strong and is only slightly flexible. If the material is carefully peeled from a portion of the nest surface, the remaining wood fibers are easily teased apart, suggesting that the material greatly aids in bonding the particles of nest material. The material also provides a waterproof coating to the nest, preventing it from being weakened should it be rained upon. Droplets of stored nectar and water for nest cooling also are prevented from soaking into the nest material.

Where the material is several layers thick, as on the stem and upper parts of the comb, it is very dark brown in color, almost perfectly matching the coloration of the adult wasps. In other species of *Mischocyttarus* the color of the nest construction secretion parallels the color of the wasps: dark-colored species (*M. injucundus*, *fitzgeraldi*, *drewseni*, *labiatus*) produce dark-colored secretion, while light-colored species (*M. leointei*, *collarellus*, *surinamensis*) produce light-colored secretion (personal observation).

VI. TROPHIC RELATIONS

A. PROTEINACEOUS FOOD

1. Method of Foraging

M. drewseni always flew close to the ground. Even if a nest was several meters above the ground, a departing forager invariably flew directly down to within half a meter of the ground, then leveled out.

The flight of a forager was one of two types. If the forager was searching for

insects she flew slowly and erratically among tall grasses and weeds, often landing for a second or so. If the forager was after pulp or nectar she usually had a few sources to which she repeatedly returned. The flights to these sources were usually direct, though a forager sometimes started out searching for insects and then ended up going after nectar. The direct flights were low, just above the "canopy" of the low herbage, and at the speed of a very fast walk, perhaps 8–10 kph.

Most foraging was done within 40–50 m of the nest, though on several occasions I followed a forager for more than 75 m before losing it, either because it flew across some barrier impassable to me (such as out over the flooded vegetation along the edge of the river), or because I confused it with a forager of *Polybia sericea*, which *M. drewseni* apparently mimics.

The following example serves to illustrate the technique most frequently used by foragers hunting for prey.

On 19 June 1968 forager no. 13 of colony 168 left the nest and flew to a dead tree that stood about 20 m from the nest. This tree was about 6 m tall and quite shrubby; most of the twigs were still intact. The leaf nodes on the twigs were enlarged, forming conspicuous swellings 5–6 mm in diameter and spaced every 5–8 cm along the otherwise linear twigs. The forager flew slowly among these twigs, pouncing frequently on the nodular swellings from a distance of a few centimeters. In each instance she merely grasped the twig with her fore- and midlegs for an instant without landing, or she would land on it for a second or less, then fly on to the next. In this manner she rapidly inspected several dozen of these nodules until she happened upon a small, well-camouflaged silk sac attached to one of the twigs. She quickly tore this open with her mandibles and removed the organism that was inside, apparently an insect pupa. The wasp chewed it for a minute or so, reducing it to a round pulpy

mass, then she returned directly to the nest with the lump held in her mandibles.

On several occasions I observed wasps attacking small prey trapped in spiders' webs. For example, no. 4 of colony 268 pounced on a male ant about 4 mm long that was hanging from a small web in a low bush. After seizing the ant the wasp hung from the spider web by her hindlegs while she chewed the ant into a small ball. She then climbed the web to a leaf and continued chewing. After a minute she flew to a nearby bush and chewed for another 30 seconds, then returned to the nest with the lump. The pattern of capturing the prey, then hanging from the web upside down while subduing the prey, and finally moving to a better position for further chewing always occurred when prey was taken from webs.

In the morning hours foragers sometimes flew along the fence surrounding the meteorological station, searching for prey trapped in the spider webs that had been built during the night between the top two strands of barbed wire. On one occasion I watched a forager fly along the top strand of wire, pouncing on every one of the wire barbs and inspecting it to see if it was prey.

In summary *M. drowseni* hunts on the wing, evidently responding to visual cues in its search for prey. The essence of the technique seems to be to fly among twigs, stems of tall grass, or anything else that provides a linear outline on which irregularities stand out against the background. Such an irregularity releases the next step, which is for the wasp to pounce quickly upon it, usually from a distance of 4–10 cm, and rapidly inspect it. The rapid pounce from flight apparently is an adaptation to minimize the chance that an alert and agile prey will escape. If the object is an appropriate prey it is quickly chewed up for carriage to the nest. Objects hanging free, such as in spiders' webs, release the same behavior.

The size of the object no doubt plays an important role in releasing the behavior.

The smallest object *M. drowseni* foragers pounced upon was an homopteran about 3 mm long, and the largest a *Trypoxylon* wasp about 15 mm long, though this latter was rejected. A forager was never observed to capture any prey that was too large to be chewed up and carried back to the nest in one trip. On the other hand, if the first prey was very small, it was sometimes completely chewed up in the field and the tiny solid fragment remaining discarded. The forager then often searched for another prey.

The following observed exception to the usual foraging technique is of interest: A forager landed on the lower part of an orb web, then began to climb up it. The spider, from its position in the center of the web, began to vibrate the web violently up and down. The wasp paused briefly, then resumed climbing toward the center. When the wasp got to within 2 cm of the spider, the spider dropped from the web. It appeared as though this act of the spider was deliberate, as if to escape the approaching wasp. The wasp then flew off. The cross-strands of the web were sticky to the touch, yet it was evidently these that the wasp was climbing on.

One of the most distinctive morphological characteristics of the genus *Mischocyttarus* is the asymmetry of the tarsal lobes of the mid- and hindlegs. The inner lobes are elongated, especially those of the distal tarsal segments. In the group *M. labiatus*, to which *M. drowseni* belongs, this feature is quite well developed. It is conceivable that this is an adaptation for climbing on spider webs in search of prey. The elongated inner lobes may hook over the fine strands of silk, acting in the manner of telephone lineman's spikes. This hypothesis accounts for the fact that the asymmetry of the tarsal lobes is most pronounced on the hindlegs and nonexistent on the forelegs. When a wasp climbs a web, the force on the hindlegs is proximal, therefore the hooks point away from the body. On the forelegs, however, the force

is distal—the wasp is hanging from these legs—and here the tarsal claws act as hooks. The inner tarsal claws of the hind and midlegs are also elongated, possibly an adaptation to hanging upside down from the web as the prey is chewed. By this argument the claws of the foretarsi might also be expected to be asymmetrical, since they are used in climbing. Their symmetry is perhaps explained by the fact that the forelegs are used extensively in the manipulation of prey after capture and during chewing, and also in cell construction. It is possible that asymmetry of the foreclaws would render them unfit for these other tasks.

On the one occasion on which I observed prey capture in another species of *Mischocyttarus*, a forager of *M. lecontei* hovered in front of a small spider (body 3–4 mm long) hanging from a single thread of silk between two leaves. The wasp then darted at the spider, grabbed it and flew backward with it, tearing it from the thread. It then landed on a nearby leaf and chewed up its prey, for about 45 seconds, then flew to another leaf to chew for another minute. It is possible that this wasp normally lands on spider webs, just as does *M. drewseni*, but did not in this instance because the single thread did not provide enough support.

The only previous record of prey-capture in *Mischocyttarus* is Williams' (1928) mention of *M. labiatus* "examining the orbs of spiders and robbing them of their smaller entangled prey." Unfortunately, he did not make clear whether the foraging wasp actually landed on the web.

On the other hand, wasps of other genera, which do not possess the asymmetrical tarsal lobes, sometimes take prey from spiders' webs but without landing on them. On two occasions I observed *Polybia occidentalis* snatch male ants from orb webs without landing, and Williams (1928) says that *Stenogaster depressigaster* regularly removes tiny insects ensnared in

spiders' webs, but without landing on the web.

This method of visually finding prey from flight, as used by *Mischocyttarus* and apparently by *Stenogaster*, differs from that used by such species as *Polybia sericea* and *Polistes canadensis*, both of which search for prey by crawling about over the leaves of grass and other low vegetation.

2. Prey

Because foragers so rapidly chewed captured prey beyond recognition, it was rare that the prey could be identified. I have seen *M. drewseni* foragers taking the following as prey: eggs from the silken case of an arthropod, probably a spider; a small moth from a spider web; male ants from spider webs; a small hemipteran nymph; a small tettigoniid grasshopper. A small weevil and a large *Trypoxylon* wasp were rejected. Small spiders when crushed and offered to wasps on the nest were readily accepted. I have never known *M. drewseni* to be attracted to fresh meat or fish, though these were often accessible to them and readily attracted wasps of certain other genera.

The only published prey records for *Mischocyttarus* are those of Snelling (1953) for *M. flavitarsis* in California. He states that their prey consists mostly of flies and caterpillars, but that they are also attracted to meat, hides, and fish. Although the prey preferences of this species appear to be different from those of *M. drewseni*, the data are not extensive enough to permit the recognition of significant differences.

3. Distribution to Adults on the Nest

When a forager returned to the nest with a masticated lump of food she usually paused for a few seconds. At this time one or more adults on the nest, including the queen and males, approached the forager to solicit the lump. The forager often turned to face her nestmate and held the lump forward, as though to offer it. The

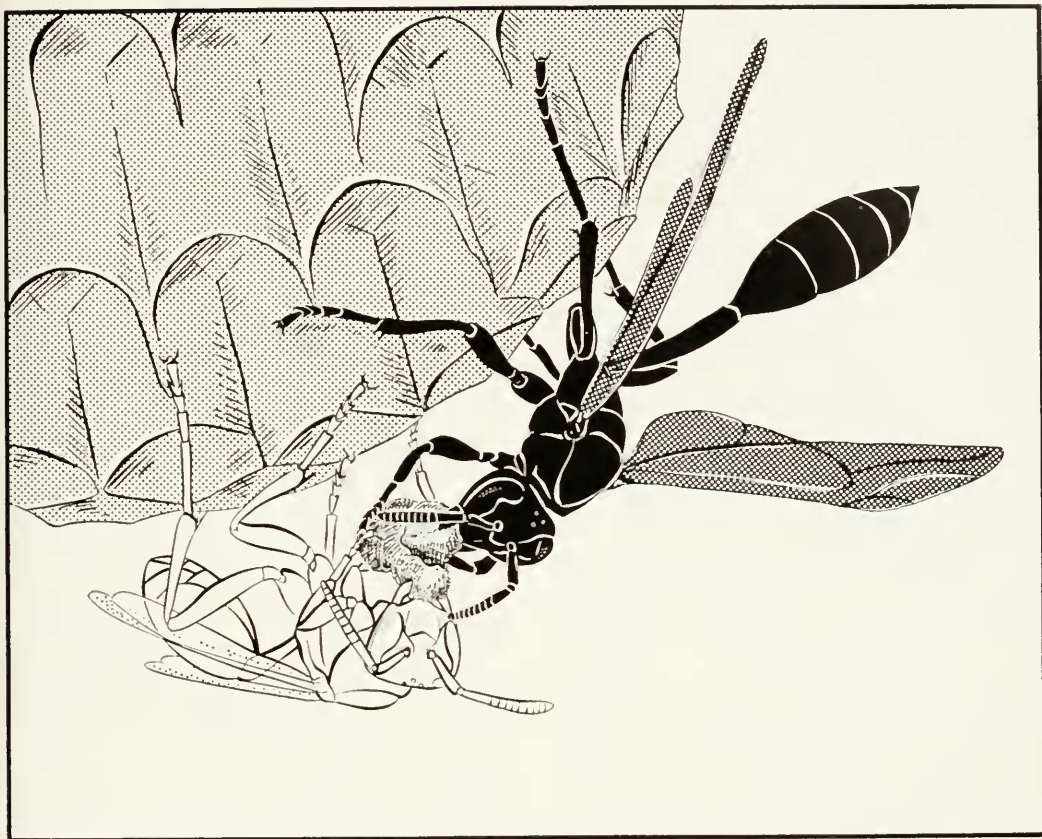


Figure 3. Sharing a lump of insect food with a nestmate. In this case the nestmate has accepted insect food brought by the forager (left), and the lump is being split. The antennae of the soliciting wasp (right) are occasionally tapped against the lump (left antenna is in motion). The antennae of the forager, on the other hand, are still. Note the submissive posture of the solicitor (head low, wings spread, abdomen raised).

solicitor antennated the food briefly, then usually took the whole lump or chewed a piece from it. Or, after tasting it, the would-be solicitor moved away without taking any. During exchange, which often lasted for half a minute, the antennae of the solicitor were used primarily to tap the lump itself and were not used against the sides of the face of the forager, as they were when liquid was being solicited (see p. 83). The forager also occasionally tapped the lump with her antennae during the exchange, though her antennae were used relatively little (Fig. 3). After the soliciting wasp had taken a part of the

lump, she in turn frequently shared it with others.

4. Distribution of Solid Insect Food to the Larvae

Lumps of food were chewed for several minutes by males and females alike. The wasp chewed forward on the lump while rotating it towards her with the forelegs; thus, when viewed from the left side, the lump rotated clockwise. During the course of chewing, the lump became somewhat smaller and considerably drier in appearance; apparently as they chewed the wasps extracted liquid from the mass and

stored it in the crop. In the case of females, the remaining solid fragment was then fed to the larger larvae. The adult adjusted her grip on the lump so that a small portion protruded in front of the mandibles, while the bulk of it was held behind. The larva removed the smaller fragment and ingested it whole, with no real chewing. The adult masticated the lump again briefly, then readjusted it prior to feeding the next larva. This was repeated until the lump was gone. Sometimes a larva did not ingest a bit of food, which then remained on its mouthparts. A worker sooner or later discovered it, removed it and chewed it briefly, then fed it to another larva.

Transfer of solid food was always directly to the mouthparts of the larva. The pair of prominent lobes on the ventral surface of the first abdominal segment of the larva was not used to support the food, as Reid (1942) suggested, and was in fact in no way involved in feeding.

Males and nonworkers who had taken lumps from foragers chewed them even longer than did workers. The remaining dry fragment was then usually fed to larvae, though it was often merely dropped.

The extraction of liquid during the chewing of solid food also occurs in *Belonogaster juncus* (Roubaud, 1916) and *Polistes fadwigae* (Yoshikawa, 1962). According to Yoshikawa (1962), workers of *P. fadwigae* tear pieces of meat from the lump with their forelegs and present them to the larvae, rather than letting the larvae remove the pieces. The passing of solid food to larvae via nestmates occurs in *Belonogaster* (Roubaud, 1916) and in *Polistes gallicus* (Heldmann, 1936). Roubaud (1916) reported that males of *Belonogaster* regularly take lumps from foragers and chew them, though he did not say whether or not they pass them on to larvae. In 75 hours of observation Heldmann (1936) saw a male of *Polistes gallicus* chew a bit of caterpillar and feed it to a larva on only one occasion. Apparently this be-

havior of males is much rarer in *P. gallicus* than in *M. drewseni*.

5. Distribution of Liquid to Adults and Larvae

After a worker had given up her lump of food, either to other adults or directly to the larvae, her nestmates often approached her to solicit for the liquid extract that she took into her crop during mastication of the prey. It was almost always the queen, males, and nonworkers who solicited this liquid; the mature workers rarely did. The mechanism of the solicitation was identical to that involved in soliciting for nectar (see p. 83).

Roubaud (1916), though observing that females of *Belonogaster juncus* extract liquid from prey by masticating it, apparently did not believe that any of this liquid is regurgitated to the larvae; he concluded that all liquid exchanges between larvae and adults are trophallactic exchanges in which the adult solicits salivary secretion from the larvae. Heldmann (1936), however, noticed that *Polistes gallicus* does feed insect juice to the larvae, and Yoshikawa (1962) reported that it is standard procedure in *Polistes fadwigae*.

In an experiment to confirm that this occurs in *M. drewseni*, I macerated small spiders with blue vegetable coloring. These "prey" were readily accepted by females on the nest and chewed in the normal manner. Initially very wet, the masses were reduced after several minutes' chewing to quite dry lumps; obviously, a good deal of the liquid had been ingested. After feeding the lumps to larvae as described above, the adults visited larvae and regurgitated the liquid, leaving a blue-colored droplet on the mouthparts of each. Of 289 foragers returning with insect food to nest 268, 70.2 percent regurgitated liquid to the larvae.

Very young larvae received proteinaceous food only in the liquid form. On a nest containing only eggs and young larvae, the queen macerated a lump of food, extracting the liquid, then discarded the lump

and visited the larvae, regurgitating the liquid to them. This same relation was confirmed for *Polistes fadwigae* by Yoshikawa (1962) and for *P. antennalis* by Morimoto (1954a). Younger larvae do not have sclerotized mouthparts and are probably unable to pull bits of solid food from the main lump held by the workers.

Though they regularly took and chewed lumps of food, extracting the juice, then sometimes fed the lump to larvae, males of *M. drewseni* never regurgitated the liquid to the larvae.

There was no way to prove that adults retained some of the liquid they had extracted from prey for their own consumption. That this is probably the case is indicated by the following observations: a) single foundresses on pre-larva nests occasionally foraged for prey, returned to the nest, masticated the lump for several minutes, then dropped the dried fragment; b) males frequently chewed lumps of insect material, evidently extracting liquid for themselves; c) 22.5 percent of the foragers who returned to nest 268 with lumps of food subsequently fed liquid neither to larvae nor to other adults, presumably keeping it for themselves. Roubaud (1916) concluded on the basis of similar evidence that adults of *Belonogaster juncus* eat insect juice. Heldmann's (1936) observations of *Polistes gallicus* suggest that the same is true of that species. Rau (1928a, 1930) reported seeing queens of *Polistes pallipes* and *P. variatus* eating insect food when no larvae were present. Elsewhere (1939) he reported that males of *P. pallipes* feed on insects brought by the foragers.

B. CARBOHYDRATE FOOD

1. Sources

Nectar was the most important source of carbohydrate. This was obtained from the buds and flowers of such plants as *Alternanthera ficoidea* (Amaranthaceae), *Hyptis atrorubens* (Labiatae), *Clidemia hirta* (Melastomataceae), and *Jatropha*

gossipifolia (Euphorbiaceae) and from the surfaces of the green seed capsules of *Heliotropium indicum* (Boraginaceae).^{*} *M. drewseni* workers also visited nipple-like extrafloral nectaries that occur on the stems of an unidentified alfalfalike legume, preferring these to the flowers of the same plant. They also sometimes obtained honeydew from the coccid *Antonina graminis*.^{**} These mealy-bugs were found at the leaf axils of a creeping grass. They were 2-3 mm long and covered with a thick white powdery coating. Protruding from the posterior end of each insect was a thin white tube about 1 cm long. The tips of these tubes often contained droplets of honeydew, which was sweet to the taste. The foraging wasps crawled down into the grass where these coccids occurred and went from one to another, collecting the droplets. There was nothing to suggest that the wasps elicited secretion of the droplets.

Snelling (1953) reported that *M. flavitarsis* in California collects nectar from the flowers of *Melilotus indica*, *M. alba* (Leguminosae) and *Helianthus bolanderi* (Compositae), and Bequaert (1933) captured a male of *M. cubensis* at flowers of *Lantana camara* (Verbenaceae) in Cuba. There is no record in the literature of any *Mischocyttarus* collecting honeydew from coccids or other Hemiptera, though Williams (1928) reported seeing *Parachartergus apicalis* in Ecuador gathered at clusters of young Membracidae, apparently attracted by the honeydew these bugs secreted. I have seen *Stelopolybia testacea* and *Pseudopolybia vespiceps* behaving the same way in Belém. Whether any of these species actually "milk" the bugs to elicit the secretion is not known.

A good source of nectar was repeatedly visited by the wasp that had discovered it, but there was apparently no communica-

^{*} All plants were determined by Dr. Murça Pires, IPEAN, Belém, Pará.

^{**} Determined by D. J. Williams, Commonwealth Inst. of Ent., London.



Figure 4. Exchange of nectar. The queen (right) is soliciting nectar from a forager. Note the position of the solicitor's antennae against the genae of the forager.

tion of its location to nestmates. I placed droplets of blue-colored sugar solution on the flowers of *Clidemia hirta*, which a marked forager was visiting for nectar. After discovering the solution the wasp made six consecutive trips in an hour and a half to the same site, stocking up on the sugar solution each time. During this time no other wasp visited the source. Three days later I repeated the experiment with another wasp from the same colony. In slightly over 3 hours she returned 20 times to the source. An interesting incident occurred when another wasp of the same colony landed near the forager while the latter was stocking up on sugar solution. The forager responded by chasing her nest-

mate from the plant, hardly an act of cooperation for the good of the colony.

2. Distribution of Nectar to Adults on the Nest

It was rarely possible to determine whether a forager brought nectar or was returning empty. If, upon landing on the nest a forager was either immediately solicited from by her nestmates or went to the larvae, it was assumed that she had brought nectar. This was precisely the behavior of foragers for whom colored sugar solution was provided in the field, as described above; that they were yielding it up to both adults and larvae at the nest was confirmed by residues of the colored

liquid on the mouthparts of the recipients after each exchange. In a small proportion of instances, foragers returned to the nest and groomed or rested without exchanging with either adults or larvae, then after some minutes visited larvae. Whether on these visits the foragers were feeding the larvae or soliciting secretion from them in trophallactic exchange was rarely clear. For purposes of analysis, it has been assumed that the latter was the case. Another uncertainty is due to the fact that foragers sometimes captured insects and chewed them up in the field, discarding the solid parts, then returned to the nest with insect juice in the crop. I suspect that this was somewhat rare, and that it is safe to assume that the majority of returns with liquid only were returns with nectar.

When a nectar forager returned to the nest, her nestmates, including the queen, nonworkers, and males, often solicited some of her liquid load. The solicitor approached the forager's head and rubbed its antennae vigorously against the mandibles, genae, and eyes of the forager as their mouthparts came into contact (Fig. 4). The forager usually held her antennae above the head of the solicitor and occasionally tapped them against the top of the head. Exchange of liquid lasted from less than a second to several seconds. There was wide variation in the vigor with which solicitation occurred. In the case of males the violence with which they solicited nectar probably depended upon how hungry they were. In the case of the queen and other females, however, it appeared to depend upon the relative dominance of the solicitor versus the forager.

Often when nectar was not shared with the nestmates (48.6 percent of the 356 observed returns), the forager appeared willing to offer to them but none approached, apparently because they were not hungry. In a few cases the forager turned away from those who approached her and went directly to the larvae.

I observed only one instance in which

a female solicitor of nectar was in turn immediately solicited from by a nestmate. In eight cases solicitors immediately fed larvae with nectar they had just received from foragers. Males were never observed to pass nectar on either to other adults or to larvae.

3. Distribution of Nectar to Larvae and Storage of Nectar

After sharing part of her nectar load with nestmates, a forager usually then fed nectar to the larvae (92.9 percent of 356 foragers). From one to many larvae were visited for from one to two seconds each. With each regurgitation of a droplet of the nectar onto the mouthparts of a larva, segments of the gaster visibly telescoped into one another, a phenomenon apparently associated with the pumping action of the crop. Vibrations of the abdomen occasionally accompanied nectar feeding (see Abdominal Vibration, p. 85).

Workers often spent more than a minute visiting each newly eclosed larva. Rau (1928a) described this kind of behavior in *Polistes pallipes* and concluded that the larvae were being fed liquid. If this is true, it is hard to understand why the visits should last so long. It may be possible that these larvae were being attended to in some other way; perhaps they were being cleaned.

Cells containing eggs were sometimes seen to contain clear droplets of nectar clinging to their walls. These droplets apparently were reserves, stored up when nectar was abundant. One of the experiments described above, in which a forager was provided with colored nectar, supports this conclusion. The forager shared its first load with a male and with larvae, leaving a blue droplet on the mouthparts of each larva visited. The next load was stored in egg cells. The third and fourth loads were shared with the queen and the larvae, and the remainder stored in egg cells. Out of the next 15 trips, she shared with nestmates 10 times, fed larvae 11 times, and stored

the remainder of each of 13 loads in egg cells. The stored droplets, in this artificial case as many as four to a cell, were gradually depleted over a period of from one to two days.

Nectar droplets were stored only in cells containing eggs, never in larval cells, though Rau (1928a) noted that *Polistes* in North America occasionally stores it in cells with larvae a few days old. The facts that droplets in a cell were often placed on the wall opposite the egg and near the mouth of the cell, and that they were usually used up before the egg hatched, indicates that they were not placed there for the newly eclosed larva to feed upon directly. Rau (1928a) reached the same conclusion for *Polistes pallipes*. I have seen nectar droplets on nests of *M. lecoinctei*, *M. injucundus*, and *M. collarellus*. The nectar-storing habit occurs in *M. injucundus* and *M. ater* in Trinidad (Vesey-Fitzgerald, 1938) and in unidentified Mexican species of *Mischocyttarus* (Rau, 1940), and is widespread in *Polistes* (Janet, 1903; Rau, 1928a, 1939; Heldmann, 1936). It occurs elsewhere in the tribe Polybiini, including *P. rejecta* and *P. occidentalis* (Vesey-Fitzgerald, 1938), and *Metapolybia* sp., reaching a culmination in *Brachygastra mellifica* and *B. lecheguana* (Schwarz, 1929). *Belonogaster juncus*, however, is said by Roubaud (1916) never to store nectar.

Heldmann (1936) noticed that the number of droplets stored in egg cells by *Polistes gallicus* was especially high with the approach of bad weather, implying that these wasps have the ability to sense the approach of a period of poor foraging and the "foresight" to lay in a supply of nectar in advance of it. I have no evidence for this in *M. drewseni*. The experiment cited above, in which I supplied a forager with a limitless supply of nectar, was done when the weather was fair for several days. This suggests that the amount of stored nectar depends primarily upon the law of supply and demand, just as Rau (1928a) concluded to be the case for *Polistes*.

That the larvae of *M. drewseni* are fed nectar has been demonstrated. The following two facts indicate that adults also feed on nectar: a) the foundress on a nest that has not yet produced any larvae sometimes collected nectar, stored the droplets in the egg cells, then depleted these droplets over a period of a day or two, presumably for her own use; b) males solicited nectar from returning foragers, as demonstrated by the experiment with colored honey solution, and apparently did not pass it on to larvae.

C. LARVAL TROPHALLAXIS

The larvae produce copious amounts of a clear secretion upon tactile stimulation of the head region. That this is a secretion and not a regurgitate was demonstrated by feeding a larva a large amount of colored sugar solution and then immediately stimulating it about the mouthparts. The resulting liquid was always clear. The source of this secretion (in *Vespa*) is said to be the labial gland (Janet, 1903; Maschwitz, 1966b).

In a test to determine the attractiveness of this secretion to adult wasps I offered droplets of it on the tip of a glass rod. Females eagerly lapped it up and licked the glass rod at some length. Alternate offerings of pure water were rejected. Males also accepted secretion thus proffered, though less eagerly than females. Using radioactive tracers, Morimoto (1960) has provided a rigorous demonstration that adult *Polistes chinensis* do take up the secretion.

Because of the difficulty of detecting which way liquid was passing between a larva and an adult, the data regarding how frequently trophallaxis occurred are only approximate. Often workers visited larvae after completing a task on the nest, after a long rest, or just before leaving the nest to forage. On such visits the workers spent five to ten seconds at each larva, much longer than the typical visits of a forager feeding nectar or insect juice. These longer visits probably involved trophallactic ex-

change. For example, on one occasion a worker returned to her nest (230) with a load of pulp and rested. After three minutes she began to heighten a cell, taking six minutes to complete the task. She groomed for 40 seconds, then visited larvae for one minute and 20 seconds, groomed briefly and left the nest. When she visited larvae in the shorter peripheral cells of the nest it was possible to see that she gently bit or mouthed the mouthparts of the larvae with her mandibles. Each larva responded either by producing a droplet of secretion, or, apparently if it has none to yield, by retracting into the cell and pulling its abdominal lobes over its head.

All the adults of the colony, including males, visited the larvae for the salivary secretion. When an adult emerged from its cocoon its first act was to visit one or two larvae, where it apparently obtained this secretion. These contacts were quite long, frequently lasting 30–60 seconds.

Ishay and Ikan (1968a, b) have found that adults of *Vespa orientalis* lack proteolytic enzymes but that larvae have them. On the basis of their work they have concluded that the larvae digest proteins in the insect food given to them by the adults and that the function of larval trophallaxis is to provide the adults with the protein digestion products. Whether or not this is true for *Vespa orientalis*, my observations suggest that it is probably not true for *M. drewseni*, since adults apparently do ingest protein as they malaxate prey, even when no larvae are present in the nest. The evidence for *M. drewseni* fits the simpler hypothesis of Maschwitz (1966b) that the larval secretion functions as a colony food reserve in times of poor foraging.

D. BEHAVIOR ASSOCIATED WITH FEEDING AND TROPHALLAXIS

1. Abdominal Vibration

Frequently, while a female visited larval cells, she vibrated her gaster rapidly up and down, flexing it at the joint between

the first and second abdominal segments. The vibrating occurred as the wasp left one cell and entered the next; during the actual contact with the larva, the abdomen was quiet. At the end of each vibration the gaster was usually bent down almost 90° at the end of the petiole, then was gradually straightened during contact with the larva. The intensity of vibration varied greatly, from a violent movement in which the ventral side of the gaster struck the surface of the nest, often producing an audible sound, to a mere perfunctory twitch or two in which no contact was made with the nest.

Abdominal vibration sometimes accompanied the feeding of liquids to larvae, as shown by experiments with colored sugar solution. However, feeding also occurred without vibration. During a series of visits a worker sometimes vibrated during the first few visits and not during later ones, or vice versa. Sometimes she did not vibrate at all. Abdominal vibrating accompanied 72 percent of visits in which insect juice was fed to larvae, and 61 percent of the nectar-feeding visits (nest 268). Again, because of the difficulty of determining whether a worker was giving or taking liquid during a visit to a particular larva, these figures may not be completely accurate.

There was a good correlation between vibration and visits to larval cells as opposed to egg cells. On several occasions I fed colored honey water to foragers, then observed them return to the nest and alternate between feeding larvae and placing droplets on the walls of egg cells. Such foragers vibrated prior to entering a larval cell, but usually not before entering an egg cell. The few exceptions to this latter rule occurred when a visit to an egg cell immediately followed a visit to a larva, as though the wasp had mistakenly expected another larva. I never saw a foundress vibrate on a nest that did not yet contain any larvae; as soon as the first larvae eclosed, however, vibration occurred.

Females occasionally vibrated during trophallactic visits to the larvae, though there are no reliable data regarding the frequency. It never accompanied the distribution of solid food to the larvae. Males never vibrated their abdomens.

2. "Pecking"

Another form of behavior, which I call "pecking," also accompanied the visiting of larvae, but much less frequently than abdominal vibration. In a typical sequence, a female inserted her head partway into an open cell, then rapidly vibrated her whole body forward and backward, giving the impression that she was violently pecking at something in the cell. This often continued for 10–30 seconds. In some cases the contact of the head with the cell wall produced an audible rattle. There was no apparent contact with the brood in the cell. This was observed a total of 14 times; in 12 cases it was done by the queen, twice by workers. It was more frequently done in egg cells (six out of ten) than in larval cells (four out of ten). In 13 out of 14 cases (93 percent) the sequence of behavior was as follows: visiting larvae and vibrating the abdomen, pecking, grooming, resting. In the other case a queen fed a lump of food to the larvae, pecked, then dominated a subordinate. Neither adults nor larvae responded in any visible way to this behavior.

3. Rubbing

A third type of behavior may be related to these other two. This resembled the rubbing of the gaster over the surface of the nest stem and back of the comb during application of the ant-repellent secretion (see below, p. 89), except that it was done on the face of the comb as a female moved over the open cells. The movement was a forward and backward "scrubbing" of the underside of the gaster against the edges of the open cells at a rate of about three times per second. Though contact was made with the nest surface, no sound

was ever detected. Such behavior often preceded visiting the larvae, especially if the individual had just come onto the face of the nest from a rest position on the side or back of the comb. There was no evident response, either on the part of larvae or other adults, to this behavior. Males never rubbed their gasters in this manner.

The function of these behavior patterns is not clear. The fact that adults placed droplets on the walls of egg cells without having vibrated indicates that this movement is not associated with the mechanics of regurgitation. There was no visible response on the part of the other adults during any of these movements. The most likely hypothesis is that it is some kind of signal to the larvae, transmitted as vibrations through the nest. Yet I could never detect any response in the larvae, neither movement nor production of larval secretion. If the adults are communicating something to the larvae, it is apparently not essential that it be done before every visit. If it is a signal, it is likely that it is transmitted to all the larvae in the nest, regardless of the position of the adult, and perhaps after a few visits with vibration all the larvae are alerted.

4. Discussion

Roubaud (1916), in describing *Belonogaster junceus*, reported that after a worker feeds a lump of food to the larvae, she goes from larva to larva, "quivering and vibrating her wings" before each visit. According to Roubaud, this causes the larvae to exude secretion, which the worker then sucks up. Rau (1928b, 1938) described three related types of behavior in *Polistes pallipes* queens. In one the gaster is vigorously moved from side to side over the open edges of the cells, causing an audible rattle. In the second, the gaster may be rubbed rapidly forward and backward over the cells. Third, the whole body may be moved rapidly forward and backward while the head is in a cell. Rau reported that all of these movements produce an

audible rasping sound, all cause the larvae to produce beads of salivary secretion, and the queens always poke their heads into the cells immediately afterwards. His interpretation was that the function of these movements is to induce the larvae to produce droplets of secretion for the adults. Heldmann (1936) reported that *Polistes gallicus* workers "rattle" the gaster vigorously from side to side over the surface of the comb, a behavior apparently identical to the first type described by Rau for *P. pallipes*. Heldmann, however, claimed that this occurred prior to giving up nectar and insect juice to larvae rather than prior to trophallactic exchange. He does not cite Rau's 1928 work.

It appears that what I call "abdominal vibration" in *M. drewseni* is analogous to the wing quivering in *Belonogaster junceus* and the side-to-side abdominal "rattling" in *Polistes pallipes*. What I call "rubbing" may be analogous to the forward-backward movement of the gaster in *Polistes pallipes* described by Rau, except that it is audible in *P. pallipes* and not in *M. drewseni*. The "pecking" behavior of *M. drewseni* appears to be identical to the third type of behavior Rau described for *P. pallipes* queens, except that in *P. pallipes* it was followed by trophallactic visits to the larvae, whereas in *M. drewseni* it was followed by grooming and resting.

My own observations agree with Heldmann's in that the "rattling" or "vibration" may precede feeding as well as trophallaxis. If this is so, then Rau's conclusion that these movements function to elicit salivary secretion from the larvae would seem not to apply to *M. drewseni* and *P. gallicus*.

A rigorously carried out comparative study of this behavior in several species of each of the three genera is badly needed. If the behavior does indeed have the same function in each of the three genera, then here may be an opportunity to study the evolution of a stereotyped behavior pattern.

TABLE 4. NATURAL CAUSES OF COLONY TERMINATION IN *M. DREWSeni*.

	Number of colonies	Percent
Declined normally	6	32
Foundress(es) died	3	16
Destroyed by ants	2	10
Destroyed by wind	1	5
Destroyed by unknown causes	7	37
	19	

VII. ENEMIES AND DEFENSE

A. ENEMIES

1. Predators of Brood

a. *Ants*. Of 19 colonies of *Mischocyttarus drewseni* that either declined or were destroyed by natural causes, two were destroyed by ants (colony 168 by *Monomorium pharaonis* and 264 by *Camponotus abdominalis*)* (Table 4). Once the ants gained access to the nest, destruction was complete down to the last egg and droplet of nectar. In each case several of the adult wasps remained near the nest for several days after the ants were gone, but would not land on it. Two adults of one colony (264) subsequently founded a new nest (295).

Records of ants attacking other species of *Mischocyttarus* included one case of *Crematogaster* sp. attacking a nest of *M. lecontei*, one case of *Crematogaster* sp. attacking a nest of *M. labiatus*, and one case of a ponerine ant attacking the brood of *M. lecontei*.

Though I witnessed no attack by *Eciton* on *Mischocyttarus*, there are records in the literature of these ants preying upon other Polistinae (Fiebrig, 1907; Wheeler, 1925; Myers, 1929; Schwarz, 1931; Vesey-Fitzgerald, 1935), and no doubt this genus constitutes a significant threat to social wasps in general.

* All ants determined by Dr. Edward O. Wilson, Biological Laboratories, Harvard University, Cambridge, Mass.

b. *Other predators.* No other predators were caught in the act of attacking the brood of *M. drewseni*. However, seven of 19 nests (37 percent) were destroyed at night such that the cells were badly damaged or the entire comb was missing, as if bitten off at the lower end of the nest stem. All these nests were small. Elsewhere (Jeanne, 1970b) I discuss the possibility that the predators were bats. Nests of *M. lecointei* were also occasionally destroyed in this manner.

Zikán (1951) claimed that the major enemies of *Mischocyttarus* colonies are birds, but that monkeys are also important. *Piranga rubra* attacks wasps' nests and eats brood (Rau, 1941b; Hamaker, 1936; Alvarez del Toro, 1950). Bertoni (1911) stated that a woodpecker (*Leuconerpes candidus*) is a serious enemy of *Polybia occidentalis*.

2. Predators of Adults

Predation of adults was rare. Spiders are probably among the most serious predators of the adult wasps. On one occasion a male *M. drewseni* was captured by the spider *Ariadna gracilis*;^{*} apparently the wasp had come near the entrance of the tubular silken nest in which the spider was hiding. On another occasion a large mygalomorph spider snatched a *Polistes canadensis* forager out of the air and paralyzed it. Yoshikawa (1963b) reported that a worker of *P. fadwigae* was caught in a spider web and killed. Vesey-Fitzgerald (1938) found an adult *M. surinamensis* captured by a salticid spider.

Other insects are probably also important enemies of adult wasps. On one occasion I discovered a large praying mantis stationed about 30 cm from a nest of *Polybia occidentalis*. As foraging wasps returned to the nest, the mantis captured and ate those that flew close to it. Vesey-

Fitzgerald (1938) noted that the fly *Nusa erythropygæ* (Asilidae) has been collected carrying *Polybia rejecta*. On the other hand, *M. drewseni* were not touched by any of the several species of dragonflies that commonly patrolled the open areas where the wasps foraged. More than once I watched large dragonflies hover a few centimeters in front of flying foragers, as though sizing them up, but they never attempted to capture the wasps, even though the slow-flying *M. drewseni* would have been easy prey.

The only record of a vertebrate preying upon adult wasps is Vesey-Fitzgerald's (1938) discovery of *M. surinamensis* in the gizzard of a swift.

3. Parasites

I never found a nest of *Mischocyttarus* containing parasitized brood. On several occasions I have seen ichneumonids land on nests of *M. drewseni* and *M. lecointei* and inspect them briefly before flying off. As far as I was able to determine none ever laid eggs. In most cases adults on the nest would spot them and move toward them, causing them to take off. Richards (1945) summarized the literature on parasites of *Mischocyttarus*.

When colonies of *M. drewseni* began to decline and empty cells began to appear, a tiny brown and yellow moth was often seen to visit the nest and run rapidly in and out of the cells. The adult wasps rarely paid any attention to these moths. Though many nests were collected after they had been abandoned, none of them ever produced any of these moths, as they might have been expected to had the moths been ovipositing.

Rau (1941a) reported that larvae of the moth *Chalcoela iphitalis* feeds on the larvae of *M. basimacula* in Mexico. This and several other species of Lepidoptera are parasitic on the larvae and pupae of *Polistes* (Rau, 1941a; Vesey-Fitzgerald, 1938), and others are scavengers on the exuviae (Swezey, 1910; Vesey-Fitzgerald, 1938).

^{*} Determined by Dr. Joseph A. Beatty, Dept. of Zoology, Southern Illinois University, Carbondale, Illinois.

Vesey-Fitzgerald (1938) found *M. surinamensis* pupae parasitized by an ichneumonid and by a dipteran. He also frequently found larvae of phorid flies in the cells of *M. labiatus*, apparently feeding on the exuviae and on the wasp pupae.

Of 760 adult *M. drewseni* marked for identification only two (0.26 percent) were stylopized. Both were females. *M. flavitarsis* from Arizona has been found stylopized (Salt and Bequaert, 1929). Ducke (1910) says that stylopization of the genus is common, but Richards (1945) found only two stylopized specimens in 1335 examined.

On two occasions dead *M. drewseni* females were found clinging to the nest in a lifelike manner. There was no sign of injury to these wasps. Presumably they died of an internal parasite or of a disease.

4. Social Parasitism

There was no evidence of social parasitism in *M. drewseni*. Zikán (1949) has discussed the possibility of social parasitism. He listed 23 species of *Mischocyttarus* that he assumed to be parasitic on closely related species, although his reasons for assuming so were based on minor morphological differences.

B. DEFENSE OF BROOD

1. Defense Against Ants

In view of the ubiquity of predaceous ants in the tropics, the relatively low rate of destruction by ants of colonies of *M. drewseni* cited above (p. 87) led me to suspect that these wasps do not rely solely on the chance that their nests will not be discovered by ants, and indeed they do not. At frequent intervals females rubbed the ventral side of the tip of the gaster along the stem and upper part of the comb of the nest for two to three seconds (Plate IV, fig. 7). At the base of the terminal (sixth) gastral sternite of female *M. drewseni* is a small, non-sclerotized area bearing a tuft of long hairs (van der Vecht, 1968). This tuft often appeared moist in living wasps,

suggesting that it carried a glandular secretion, which is brushed onto the nest stem. The following experiment pointed to the conclusion that this secretion is effective in keeping at least some predaceous ants from traversing the nest stem and discovering the brood.

Series of "artificial nests" were set up by fastening a row of glass capillary tubes 65 mm long in a vertical position (simulating the nest stem) and providing them with small squares of Brazil nutmeat at their upper ends (simulating brood). Half of the tubes were provided with smears of secretion 10–15 mm long by rubbing them against the tuft of hair of from one to four living wasps. Alternate tubes were left unsmeared as controls. As ants (*Monomorium pharaonis* was used in all tests) began to explore each tube the following data were recorded: (1) the number of ants to ascend the tube partway, turn around and descend, and (2) the number of ants to reach the nut meat at the top of the tube. With few exceptions, the ants failing to reach the bait on the secretion-smeared tubes stopped and turned around at the smear itself. When ten ants had reached the bait on a given tube the number of ants to ascend only partway was totalled. In 38 trials (19 smeared tubes vs. 19 unsmeared tubes) the number of ants turning back before reaching the bait was significantly greater for the smeared tubes than for the unsmeared tubes ($P < .001$).

A second set of trials was run in which the control tubes were smeared with one of several materials, including water, Vaseline, salivary fluid of *M. drewseni*, or rubbed against the fourth or fifth sternite of *M. drewseni*. In 30 trials (15 secretion-smeared vs. 15 control-smeared tubes) the number of ants stopping at the smear of secretion was significantly greater than those stopping at the smear of control substance ($P < .001$). (For data and a more detailed description of these experiments see Jeanne, 1970a.)

Tests involving actual nests of *M. drewseni* bear out the conclusion reached from

these experiments. Wasp larvae removed from their cells and affixed to the substrate around the base of attachment of an active nest attracted *Monomorium pharaonis* in large numbers in a matter of hours, yet none of these ants succeeded in getting down the nest stem; though many attempted (96 in 11 minutes in one case), none got more than a few millimeters before turning back. The results were the same if the adult wasps were removed from the nest so they could not actively defend it.

It is clear that the secretion smeared on the nest stem is an effective repellent to at least some ants. Whether the effect is due to the chemical or physical nature of the substance is not certain. However, two observations suggest that it is the chemical nature of the secretion to which the ants respond. First, very little secretion is applied to the nest stem; so little, in fact, that the stem appears completely dry and clean both to the eye and to the touch. Second, when ants contacted a smear of the secretion on the experimental glass tubes, they often retracted violently from it and groomed their antennae extensively, indicating that the smear was "distasteful" to them. The control materials never elicited such behavior.

The structure of the nest and the morphology of the adult wasp have apparently co-evolved toward the optimization of this defense behavior. The nest stem is long, providing a long barrier for ants to cross. The first abdominal segment of *M. dreuseni* is elongated, enabling the application of secretion over most of the length of the stem. The small diameter of the stem, and its smooth, nonabsorbent surface are features that minimize the amount of secretion required to keep the stem adequately covered.

It is during the pre-emergence stage of colony development that colonies of *M. dreuseni* are most vulnerable to ants, since the founding female must leave the nest unattended to forage. Defense of the type

evolved by *M. dreuseni* enables her to do so without increasing the risk that the nest will be discovered by ants during her absence. The repellent properties of the secretion are probably ineffective against army ants (*Eciton* spp.), which forage en masse. But my impression is that the chance that a nest will fall in the path of such a raid is low enough for most colonies to mature and produce sexuals before being attacked.

2. Alarm Reaction to Flying Insects

Adults on the nest respond to insects flying near the nest to a degree corresponding to how close and how persistently the intruder approaches. Probably size and proximity of the insect are directly correlated in evoking a given response; thus, a smaller insect must be closer than a larger one to evoke the same degree of response. If the insect was relatively far from the nest (about 25–50 cm for a large insect such as *Polistes*) the female *M. dreuseni* merely turned toward the movement. If the insect came closer, the wasp spread her wings and darted at it. If the intruder persisted, or came very close, the wasp flew at it and drove it away. This latter behavior occurred only in response to larger insects. There was apparently no discrimination of form or coloration by the wasps; they appeared to respond indiscriminantly to movement.

Each wasp on the nest responded to a flying insect directly and independently of the response of nestmates; that is, each wasp had to see the movement herself to respond. Wasps on the opposite side of the nest could not see the movement and did not respond (but compare the reaction to large objects, below). Adults on the nest were not particularly alert to smaller flying insects. In several instances small insects (such as mosquitos) flew close to the nest, or even landed on it, apparently without being seen by the wasps.

The "darting and wing-flipping" that *Polistes fuscatus* performs in the presence

of the ichneumonid parasite *Pachysomoides fulvus* has been interpreted as a "special parasite alarm" behavior (Eberhard, 1969). No such behavior occurred in *Mischocyttarus drewseni*, though the buzzing of the wings in the presence of large intruders (see next section) may be homologous with it.

3. Alarm Reaction to Large Objects

If a large object, such as the investigator's hand, was moved toward a nest, the first response of the wasps was to turn to face the movement. If the object continued to approach, the wasps first spread their wings, then raised the anterior ends of their bodies, lifting the forelegs from the nest (Plate IV, fig. 8). With more intense disturbance, they bent their abdomens around to one side and buzzed their wings. Finally, one or more of them sometimes flew at the object and attempted to sting it. Newly emerged females less than 24 hours old as well as mature adults exhibited this defensive behavior.

While wasps were responding to a disturbance by bending their abdomens to the side and buzzing their wings, a strong odor, resembling soap or stale saltines, was often detectable. The same odor was detected at the site of a sting, where it lasted for a minute or two. This substance may be an alarm odor. It is possible that the source of such a pheromone is a gland that opens in the sting chamber, and by bending the abdomen to the side and buzzing the wings the wasps disperse the chemical. Rau (1939) noticed that *Polistes variatus* spreads its wings and produces a "pleasantly sweetish" odor when disturbed.

If an object approached the nest such that the wasps on the opposite side could not see it, these wasps did not show the alarm behavior unless those who could see the object buzzed their wings. Then all the wasps on the nest became alert, spread their wings and raised their forelegs from the nest. If the buzzing stopped, these others began to settle down. Apparently

either the vibration of the buzzing or the dispersal of odor communicates alarm. This may be homologous to the "wing-flipping" observed in *Polistes fuscatus* (Eberhard, 1969).

During the course of the study I was stung by *M. drewseni* eight times. The pain varied considerably, probably in proportion to the amount of venom injected, but never lasted more than a few minutes. In a typical sting, received on the arm, the pain reached a maximum after several seconds, then began to subside gradually. There was a small red dot, representing the puncture of the sting. After ten minutes a swollen welt had increased to 7–8 mm in diameter. After half an hour this had changed to a slightly swollen red area 3 cm in diameter. After six hours only the small red puncture remained; there was no pain in the area, even when pressed.

4. Variations in Aggressiveness

There was often a marked increase in the aggressiveness of a colony in the late afternoon and early evening. At this time of day it was often not possible to approach a mature colony, however carefully, without alarming the adults and sometimes causing one or more to fly off at me and attempt to sting. The same colonies had a much higher threshold of aggressiveness during the day.

There was a definite positive correlation of aggressiveness with number of adults on a nest. Sometimes it was difficult to approach closely a small, single-foundress nest without causing the adult to flee. The same colony later in its development was often impossible to approach without eliciting aggressive behavior.

VIII. DIVISION OF LABOR

A. SPECIALIZATION ACCORDING TO CASTE

1. Activities of the Queen versus the Workers

Tables 5 and 6 give the rates at which various tasks were performed by co-found-

TABLE 5. Division of labor among co-foundresses of colony 258. Rates are given as the number of times the task was performed per hour of observation. Numbers in parentheses give the absolute number of times the task was performed. Adults are arranged in order of dominance rank. Number 66 is the queen.

Adult	Hrs. obs.	Foraging			Cell Construction		Rubbing	Mouthing	No. eggs laid	Rate of domin.
		Pulp	Insect	Nectar	Init.	Height.				
66	47	.04(2)	0	.02(1)	0	.08(4)	0	.02(1)	13	.44(2)
57	46	.10(5)	.04(2)	.06(3)	0	.13(6)	.09(4)	.06(3)	2	.06(3)
60	28	.16(6)	0	.31(12)	.05(2)	.10(4)	.18(7)	.05(2)	1	.08(3)
54	45	.09(4)	.02(1)	.22(10)	0	.09(4)	.04(2)	.02(1)	0	.02(1)
74	46	.04(2)	.11(5)	.13(6)	0	.04(2)	.04(2)	.02(1)	0	0
35	46	.15(7)	.04(2)	.26(12)	.02(1)	.13(6)	.11(5)	.06(3)	0	0
16	16	0	0	.32(5)	0	0	0	.06(1)	0	0
21	16	0	0	.06(1)	0	0	0	0	0	0
No. times task performed		(26)	(10)	(50)	(3)	(26)	(20)	(12)	16	(28)

resses of representative pre-emergence colonies (258 and 310). Table 7 gives the same data for a representative postemergence colony (268). In both pre-emergence and postemergence colonies the queen was the primary egg-layer. The task of preparing a previously used cell to receive a fresh egg involved removing the torn silken cap and was virtually always done by the egg-layer immediately before oviposition.

In any dominance-subordinance encounter the queen was always dominant. Usually the queen was involved in dominance interactions more frequently than her subordinates (exception: worker no. 2 on

nest 268 dominated her subordinates more frequently than did the queen; Table 7).

The queen on 310 foraged for insects as well as for pulp, though pulp predominated in her loads (Table 6). Neither the queen on 258 nor any of the three queens on 268 ever foraged for insects, though of 16 loads foraged by six queens on other postemergence nests, four were insects. Thus, although pulp predominated among their loads, queens did not specialize in pulp foraging to the exclusion of insect food, as do queens of *Polistes fuscatus*, *P. canadensis* (Eberhard, 1969), and *P. gallicus* (Pardi, 1951).

TABLE 6. Division of labor among co-foundresses of colony 310. Rates are given as the number of times the task was performed per hour of observation. Number of times each task was performed is given in parentheses. Adults are arranged in order of emergence on the parent nest (23), except that the queen (no. 50) is given first. The rates of domination were too low to establish a linear hierarchy among the co-foundresses.

Adult	Hrs. obs.	Foraging			Cell Construction		Rubbing	Mouthing	No. eggs laid	Rate of domin.
		Pulp	Insect	Nectar	Init.	Height.				
50	39	.43(17)	.07(3)	0	0	.46(18)	.08(3)	0	8	.08(3)
49	39	.10(4)	.15(6)	.31(12)	.02(1)	.07(3)	.10(4)	0	0	0
57	39	.02(1)	.04(2)	.26(10)	.02(1)	0	.23(9)	0	0	0
47	25	.04(1)	0	.04(1)	0	.04(1)	.04(1)	0	0	0
54	25	.16(4)	.04(1)	.12(3)	.04(1)	.12(3)	.08(2)	0	0	0
No. times task performed		(27)	(12)	(26)	(3)	(25)	(19)	0	8	(3)

TABLE 7. Division of labor among queens and workers of colony 268. Data are from post-emergence stage only. Rates are given as the number of times the task was performed per hour of observation. Number of times each task was performed is given in parentheses. Adults are arranged in order of emergence. Numbers 1, 8, and 36 are queens.

Adult	Hrs. obs.	Foraging			Cell Construction				No. eggs laid	Rate of domin.
		Pulp	Insect	Nectar	Init.	Height.	Rubbing	Mouthing		
1	51	.02(1)	0	.02(1)	.02(1)	.12(6)	0	.02(1)	8	.45(23)
2	45	.24(11)	.11(5)	.22(10)	0	.24(11)	.18(8)	.04(2)	0	.51(23)
3	91	.05(5)	.10(9)	.18(16)	0	.04(4)	.05(5)	0	0	.01(1)
4	34	.50(17)	.47(16)	.24(8)	0	.50(17)	.32(11)	.06(2)	0	0
5	93	.05(5)	.40(37)	.20(18)	0	.04(4)	.06(6)	.03(3)	0	.01(1)
6	124	.04(6)	.11(14)	.27(34)	0	.02(3)	.04(5)	.01(1)	0	0
7	46	.30(14)	.24(11)	.17(8)	0	.30(14)	.02(1)	.02(1)	0	.13(6)
8	82	.18(15)	0	0	.02(2)	.40(33)	.01(1)	0	22	1.91(157)
9	117	.04(5)	.20(23)	.24(28)	0	.03(4)	.02(2)	0	0	0
10	48	.18(9)	.23(11)	.73(35)	0	.19(9)	.02(1)	.02(1)	0	.04(2)
11	114	.20(23)	.13(15)	.32(37)	0	.16(19)	0	0	0	.01(1)
20	99	.16(16)	.20(20)	.23(23)	0	.12(12)	0	.01(1)	0	.04(4)
22	88	.11(10)	.33(29)	.23(20)	0	.09(8)	.03(3)	.02(2)	0	.01(1)
27	53	.21(11)	.32(17)	.19(10)	0	.21(11)	0	0	0	.19(10)
28	50	.10(5)	.12(6)	.32(16)	0	.10(5)	.02(1)	0	0	.06(3)
29	53	.06(3)	0	.11(6)	0	.06(3)	.06(3)	0	0	.08(4)
32	70	.08(6)	.07(5)	.24(17)	0	.08(6)	0	0	0	.03(2)
35	86	.03(3)	.08(7)	.19(16)	0	.03(3)	.02(2)	0	0	.08(7)
36	86	.01(1)	0	0	.03(3)	.03(3)	0	0	14	1.51(130)
49	16	.12(2)	.12(2)	.06(1)	0	.06(1)	0	.06(1)	0	0
52	51	.03(2)	.02(1)	.20(10)	0	.04(2)	0	0	1	0
53	51	0	.02(1)	.33(17)	0	0	.02(1)	0	0	0
73	35	.20(7)	.51(18)	.26(9)	0	.14(5)	0	0	0	0
86	27	.15(4)	.26(7)	.15(4)	0	.15(4)	0	0	0	.04(1)
96	22	.09(2)	.09(2)	.04(1)	0	.09(2)	0	0	0	.04(1)
98	20	.05(1)	.05(1)	.10(2)	0	.05(1)	0	0	0	.05(1)
107	16	0	0	.06(2)	0	0	0	0	0	0
No. times task performed		(184)	(257)	(333)	(6)	(190)	(50)	(15)	45	(378)

None of the six cell initiations observed on pre-emergence nests were done by queens (Tables 5 and 6). On the other hand, all five of those seen on postemergence nest 268 were performed by queens (Table 7). The two cell initiations seen on all other postemergence nests were done by workers. Initiation of new cells by subordinates occurs in *Polistes fuscatus*, but not in the tropical *P. canadensis* (Eberhard, 1969).

A forager returning with pulp usually applied it to the nest herself. However, 40 loads out of 195 (20 percent) were shared. Each shared load was always shared (never given up entire) with only one nestmate and that nestmate was without exception the queen.

Most or all of the pulp used by the queens of pre-emergence colonies was foraged by them, while most of the pulp used by queens of postemergence colonies was received from foragers.

Lumps of food were more frequently shared with nestmates than were pulp loads. Of 311 loads brought to three nests, 223 (72 percent) were shared. The remaining 28 percent were fed directly to larvae by the forager. Each load was shared with an average of 1.9 nestmates (range: 1–5), and the forager often gave up the entire load, keeping none for herself. They were shared with any nestmate, including queen, nonworkers, and males. On one nest (268) 208 loads of insect food were shared with 294 nestmates, of which 84 (29 percent) were queens. In 79 percent of the cases queens masticated the lumps, then fed them to larvae; in 21 percent they passed them on to other adults.

Queens foraged for nectar at very low rates or not at all. Co-foundresses and workers, however, foraged at high rates. Of 356 loads of nectar, 183 (51 percent) were shared with an average of 1.5 nestmates each (range: 1–5). Queens solicited nectar from returning foragers at high rates. Their subordinates solicited nectar at rates decreasing roughly with their social rank. Of 289 recipients of nectar, 41 (14 percent) were queens and virtually all the rest were males and nonworkers.

Queens on all nests rubbed and mouthed the nest stem little or not at all.

Fanning the nest when the temperature reached a critical point was done by queens, workers, and occasionally by nonworkers and males. Bringing water and spreading it over the nest for cooling was done primarily by workers.

In summary, queens: 1) were dominant and usually dominated at higher rates than subordinates; 2) were the primary egg-layers; 3) prepared used cells to receive eggs; 4) foraged primarily for pulp, rarely for nectar or insects; 5) initiated cells on postemergence nests, but not on pre-emergence nests; 6) heightened cells; 7) distributed insect food to larvae and nestmates; 8) solicited pulp, insects and nectar from returning foragers; 9) rarely mouthed or rubbed the nest stem; and, 10) some-

times fanned the nest and hauled water for cooling.

Workers: 1) were subordinate; 2) foraged for pulp, insects and nectar; 3) distributed insects and nectar to nestmates and larvae; 4) initiated cells; 5) heightened cell walls; and, 6) fanned the nest and hauled water.

Thus pre-emergence colonies differed from postemergence colonies in that in pre-emergence colonies: 1) subordinates sometimes oviposited; 2) subordinates rather than the queen initiated cells; 3) queens themselves foraged for most of the pulp they applied to the nest; and, 4) subordinates as well as the queen frequently solicited nectar and solid food from returning foragers.

2. Activities of Nonworkers

Nonworkers obtained food by soliciting insect food or nectar from returning foragers and by soliciting secretion from larvae. They chewed solid food, extracting liquid, then either passed the remaining fragments on to nestmates, fed them to larvae, or dropped them (especially in the case of small fragments). Nonworkers often left the nest for varying periods, presumably either to forage for themselves or to mate with males. When they returned they did not feed larvae. They fanned the nest when it was heated above a certain critical temperature. They also showed defensive behavior in response to intruders. Finally, they took part in dominance interactions.

It is necessary here to emphasize that the distinction between "workers" and "nonworkers" is somewhat artificial. Nonworkers by definition do not forage for pulp or insects. Yet individuals that came under the nonworker definition sometimes performed other workerlike tasks. Thus, on six occasions nonworkers returned to the nest, apparently with nectar, which they gave up to nestmates or to larvae. On another occasion a nonworker chewed down the walls of a recently emptied cell

and applied the pulp elsewhere on the nest. Nonworkers were twice seen to bring water to the nest for cooling and to fan the nest on five occasions. On the other hand, some "workers" worked at extremely low rates. Such cases suggest that "worker" behavior and "nonworker" behavior may be continuous, and that the distinction between "worker-ness" and "nonworker-ness" is a matter of degree.

Despite such uncertainties, however, the two castes do seem to exist. The criterion used to define a worker, *i.e.*, returns to nest with a solid load, was chosen because it was easy to apply and was consistent with Eberhard's (1969) terminology. It has the virtue of including in the worker category approximately those who contribute to the growth and maintenance of the colony by supplying materials. Nectar foraging was not included in the definition of worker status because of the difficulty of determining with certainty when a forager was actually returning with nectar in its crop. To judge from Table 7, however, which includes nectar foraging rates based on somewhat arbitrary criteria (see *Trophic Relations*, p. 76 ff.), pulp and insect foragers were also nectar foragers. The six cases mentioned in which nonworkers definitely returned with nectar involved only four individuals out of a total of 43 nonworkers. It is quite possible that, had they been observed more extensively, these four would have been seen to forage for pulp and insects as well, and could have been called workers. Thus, if anything, the limited definition of worker leads to the inclusion of some true workers in the nonworker class.

3. Activities of Males

Males solicited insect food and nectar from returning foragers for their own consumption. When males were abundant on a nest, they often mobbed returning foragers, giving the impression that they were hungry. They did not pass nectar on to larvae, though often after they chewed a

bit of insect material for several minutes they fed it to a larva. They seemed to rely primarily on foragers for food and solicited from larvae relatively infrequently. Males fanned their wings when the sun struck them on the nest. They sometimes grasped a female with the legs or bit a member with the mandibles and held on for several minutes. The meaning of this is not clear.

B. TEMPORAL SEPARATION OF TASKS DURING THE DAY

Certain tasks were performed more frequently at some times of day than at others. Figure 5 plots rate at which four tasks were performed against hour of the day.

Pulp foraging (Fig. 5A) began early in the day and continued at a fairly steady rate until 13:00 hours, after which it declined. This may have been related to the availability of water, which was used in the removal of pulp from plant stems, planks, etc. In the early morning (06:00–08:00) such substrates were frequently quite moist from condensation of dew during the night. Later in the day, when pulp sources had dried out, foragers sought water from wet mud, droplets trapped in leaf axils, and other places where rain-water was stored. Such sources were more likely to dry up during the hottest part of the day (early afternoon) than at other times. This may help to explain low rates of pulp foraging from 14:00 on.

Insect foraging (Fig. 5B) began an hour or so later in the morning than pulp foraging and remained high until midafternoon, when it tapered off. This pattern may be related to the activity patterns of insects sought as prey, though there are no data bearing on this.

The limitation of mouthing the nest stem strictly to the early morning hours was most striking (Fig. 5C). This was the first task the workers performed at the beginning of daily activity. It was rarely performed after 08:30 and never after 11:00. Deleurance (1957) found the same daily

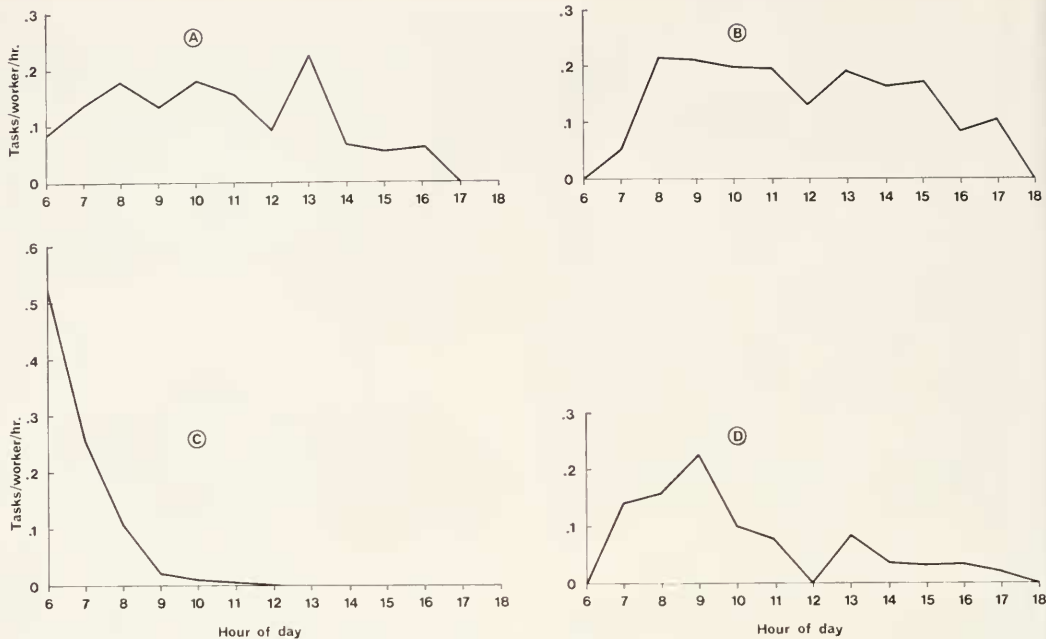


Figure 5. Temporal division of labor. A. Foraging for pulp. B. Foraging for insects. C. Mouthing the nest stem (application of nest construction secretion). D. Rubbing the nest stem (application of ant repellent secretion).

rhythm of petiole construction to exist in *Polistes gallicus* reared in the laboratory. The significance, I think, is clear. Applying a new layer of nest construction material to the nest stem effectively covers up the previous day's coat of defense secretion. In terms of the most efficient use of the defense secretion, it is obviously best to apply the entire day's supply of nest construction secretion to the stem first, then put the defensive secretion on top of that, rather than mixing the two activities throughout the day. The heaviest concentration of rubbing activity did indeed closely follow mouthing (Fig. 5D).

IX. DOMINANCE AND CASTE DETERMINATION

A. THE NATURE OF DOMINANCE-SUBORDINANCE BEHAVIOR

In encounters between two females of a colony one of the pair usually dominated over the other. The violence with which one individual dominated another varied,

as did the degree to which the subordinate individual showed submissive behavior.

In the mildest form of domination the dominant wasp merely turned and darted or rushed toward the subordinate but did not make contact with it. The subordinate either did not respond at all, merely flinched, or moved away.

In the most typical form of domination the dominant rushed at the subordinate and violently mouthed its body with the mandibles while antennating it vigorously. This was often accompanied by a rapid forward-and-backward "pecking" motion of the entire body. The face and top of the head of the subordinate were most frequently attacked in this way, but the thorax, wing bases, abdomen, and legs were also attacked. The most typical response of the subordinate was what I call the "submissive posture." This is not the same as Pardi's "position of akinesis" (Pardi, 1948b), in which the body is appressed to the nest, head bent and antennae and legs in flexion. The submissive

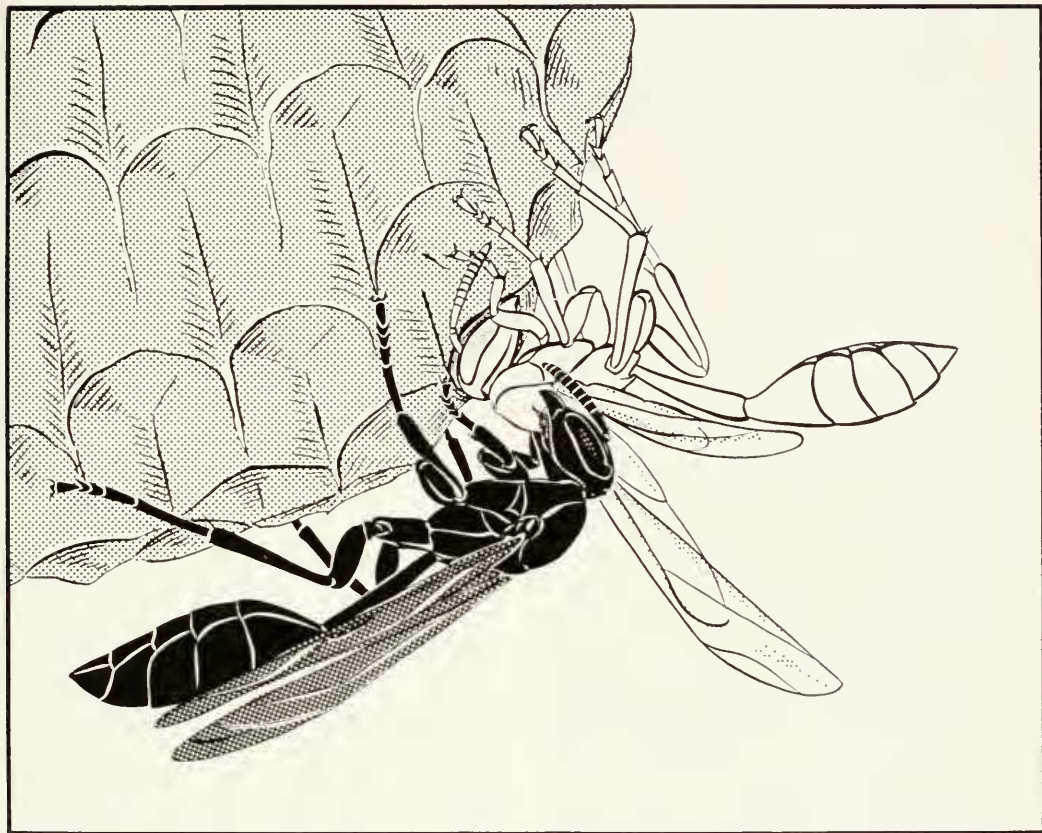


Figure 6. Domination. The dominating wasp (left) is violently mouthing the thorax of the subordinate with her mandibles. The subordinate is responding with an extremely submissive posture: head down against the nest surface, abdomen raised, and wings spread.

posture in *M. drewseni* in its least pronounced form consisted in bending the head down and raising the abdomen slightly. In the most extreme form the rear end of the body was raised so that the long axis of the body was nearly perpendicular to the nest surface, the front of the head pressed against the nest surface, and the wings spread (Fig. 6).

If the subordinate tried to escape, the dominant often chased after her. Sometimes a very dominant individual stopped dominating a subordinate and stood directly before it for several seconds as if watching it. During this time the subordinate usually remained in the submissive posture. If the subordinate moved to come

out of its submissive posture, the dominant immediately rushed forward and mouthed it violently again. This was often repeated several times before the dominant finally moved away. An extremely subordinate wasp sometimes remained in the submissive posture for a minute or more after the dominant wasp had moved away. Such an individual was sensitive to movement of any wasp near it, responding by raising its abdomen and depressing its head even more.

During the intervals in which the dominant wasp watched the subordinate, the dominant often vibrated its gaster in a rapid up-and-down motion, causing an audible rattle as it struck the nest surface.

This "vibration" was of the same sort that often accompanied the visiting of larvae (see Trophic Relations, p. 76 ff.). The vibration itself had no visible effect on the subordinate. In a few instances a subordinate responded to this form of domination by regurgitating a small droplet of liquid from its crop and offering it to the dominant. The dominant sometimes lapped it up, but usually it did not. A less submissive individual, such as an older worker, when attacked by a dominant wasp, merely stopped what it was doing and lowered its head slightly until the domination stopped.

In some cases the dominant individual, after mouthing the subordinate, grasped an antenna, a wing, or a leg in its mandibles, tugged on it with a jerking motion for several seconds, then merely held onto it for as long as a minute without moving. The subordinate at first did not move, but then usually gingerly tried to extricate itself by pulling away. Sometimes this caused the dominant to renew its vigorous tugging on the member, though often the subordinate managed to escape.

In the most severe form of domination the dominant wasp grappled with a subordinate, grasping it with the legs around the body while trying to bite or even sting it. The subordinate either remained passive or tried to escape. On rare occasions this struggle was so violent as to cause the pair to fall from the nest, and on one occasion resulted in the death of one of the pair.

Newly emerged adults (one to two days old) moved about the nest but little and rested with their bodies appressed to the nest surface. They were rarely dominated. Their response to the rare dominations they received and to males seeking to solicit food was to press the body even closer to the nest and draw the legs in close to the body. This resembled akinesis in *Polistes gallicus* (Pardi, 1948b). As they matured they began to respond to domination with the typical submissive posture.

B. THE SOLICITATION-DOMINATION CONTINUUM

Often it was not possible to determine whether an interaction was a domination or whether one wasp was soliciting liquid food from the other. The initiator of an interaction often vigorously mouthed the mouthparts of a forager, to which the forager usually responded by moderate submission. In such encounters the initiator was obviously the more dominant, yet an exchange of fluid sometimes occurred. A difficulty arises in trying to classify such encounters as either solicitations or dominations. The most natural interpretation seems to be one that places the two phenomena on the same continuum.

At one end of the scale were cases of obvious solicitation, in which a soliciting wasp approached a just-returned forager and mouthed its mouthparts, its head lower than the forager's, to which the forager responded by regurgitating a droplet. In encounters of this type the soliciting wasp was evidently less dominant than the forager. At the other end of the scale were clear-cut cases of domination, such as when the queen violently attacked a subordinate and mouthed it about the head and thorax, ignoring any attempts on the part of the subordinate to offer a droplet of food. Between these two extremes the behavior of each participant seemed to vary continuously in degree of dominance. The behavior of the initiator ranged from simple begging at the low end of the scale to out-and-out domination at the upper end. The behavior of the other ranged from extreme submission and attempts to escape at the low end to unsubmissive yielding of a droplet at the upper end.

Males commonly approached returning foragers as well as other females on the nest, and even other males, to beg for regurgitated droplets by mouthing and antennating the mandibles of the donor. Often the female responded submissively, either by assuming the submissive posture, or by escaping to another part of the nest.

Such encounters were often quite violent and were frequently indistinguishable from domination of one female by another. The females appeared to be acting submissively to the males. It is possible that by acting in a submissive way the females may indicate to the solicitor that they have no liquid to give.

The point I wish to stress is the apparent continuity between "soliciting" for food and "dominating" subordinates. This suggests that dominance behavior had its origins in trophic exchanges between nest-mates. At least trophic exchanges often seem to provide the context in which differentially aggressive individuals come into the repeated contact that, according to West (1967), is a necessary condition for the establishment of a dominance order. Though West has provided a theoretical explanation of the adaptive value of a dominance hierarchy, the phylogeny of the phenomenon remains unexplored.

C. PATTERNS OF DOMINANT AND SUBORDINATE BEHAVIOR

1. Rates of Dominance Interactions

Compared with *Polistes gallicus*, the rate at which dominance encounters occurred in *M. drewseni* was low. Most of the contacts between co-foundresses were peaceful exchanges of pulp or food. On most nests, the number of dominations among co-foundresses was less than 0.10 domination per female per hour of observations (Table 8). In contrast to this, among the seven co-foundresses of a comparable pre-emergence colony of *P. gallicus* there were 109 interactions in only eight hours (Pardi, 1946), a rate of 1.94 dominations per female per hour, or about 20 times the rate in *M. drewseni*.

In *M. drewseni* many individuals on multiple-foundress pre-emergence nests were not involved at all in dominance interactions. The interactions in colony 258, for example, involved only nine (32 percent) of the 28 possible pair combi-

TABLE 8. MEAN FREQUENCY OF DOMINANCE INTERACTIONS ON MULTIPLE-FOUNDRESS COLONIES IN THE PRE-EMERGENCE STAGE OF *M. DREWSeni*. DAYS OBSERVED GIVE THE SPAN OVER WHICH OBSERVATIONS WERE MADE. RATE OF DOMINATION IS EXPRESSED IN NUMBER OF DOMINATIONS PER WASP PER HOUR OF OBSERVATION.

Colony no.	No. co-foundresses	No. dominations	Hrs. obs.	Days obs.	Rate of domination
223	2	0	17.8	31	0
237	3	0	4.8	8	0
258	8	27	46.0	17	.07
295	2	1	11.9	27	.04
310	5	3	39.0	36	.02
421	2	1	2.2	36	.22

nations (Table 9), and in colony 310 only two (20 percent) of the ten possible pairs (Table 10). On a pre-emergence nest of *P. gallicus* with seven co-foundresses observed by Pardi (1946), 20 (95 percent) of the 21 possible pair interactions occurred.

Domination interactions among female offspring of a colony also occurred at a lower rate than in *P. gallicus*. Table 11 gives the number of interactions for each pair of females on colony 268. In 148 hours of observation over 106 days there were only 434 dominations among 70 females. (Not all of the females were present on the nest for the entire period.) This compares with 589 dominations observed in only 14 hours and 45 minutes among nine females of a colony of *P. gallicus* (Pardi, 1946).

2. Age Distribution of Dominant and Subordinate Behavior on Established Colonies

Dominance interactions appeared to involve primarily the queen and the younger offspring at any given time. Though workers may live for 11 weeks or longer, it was primarily during their first ten days that they were involved in dominance encounters, both as dominant and as subordinate. A newly emerged female required about three days to "mature." During this time she remained on the nest and was largely

TABLE 2. Numbers of dominance interactions among pairs of *Q.*-foundresses on colony 38. Based on 46 hours of observation from 15 July to 31 July 1968. Frequency of domination and submission is expressed as number of interactions per hour of observation.

Subordinate individual	Dominant individual								Total submissions	Mean frequency submission	Total individuals submitted to
	66	57	60	54	74	35	16	21			
66									0		0
57	11								11	.24	1
60	6	3							9	.24	-
54	1	-	-						1	.02	1
74	2	-	1	1					4	.09	3
35	-	-	1	-	-				2	.06	1
16	-	-	1	-	-	-			3	.02	1
21	-	-	-	-	-	-	-		0		0
Total dominations	20	3	3	1	2	0	0	0	27		
Mean frequency domination	.44	.06	.08	.02	.07	0	0	0			
Total individuals dominated	4	1	3	1	1	0	0	0			

inactive, except to solicit food from passing foragers or secretion from larvae. She was practically ignored as an object of domination by the queen and other dominant nestmates. In the days following, however,

she was dominated more and more frequently, until her fifth day, when the average rate of domination reached a maximum of over one domination per hour. From day five the rate at which she was dominated

TABLE 3. Numbers of dominance interactions among pairs of *Q.*-foundresses on colony 39. Based on 46 hours of observation from 15 September to 15 November 1968. Frequency of domination and submission is expressed as number of interactions per hour of observation.

Subordinate individual	Dominant individual					Total submissions	Mean frequency submission	Total individuals submitted to
	41	49	57	47	54			
41						0	0	0
49	-					2	.05	1
57	1	-				1	.04	1
47	-	-	-			0	0	0
54	-	-	-	-		0	0	0
Total dominations	1	0	0	0	0	1		
Mean frequency domination	.02	0	0	0	0			
Total individuals dominated	1	0	0	0	0			

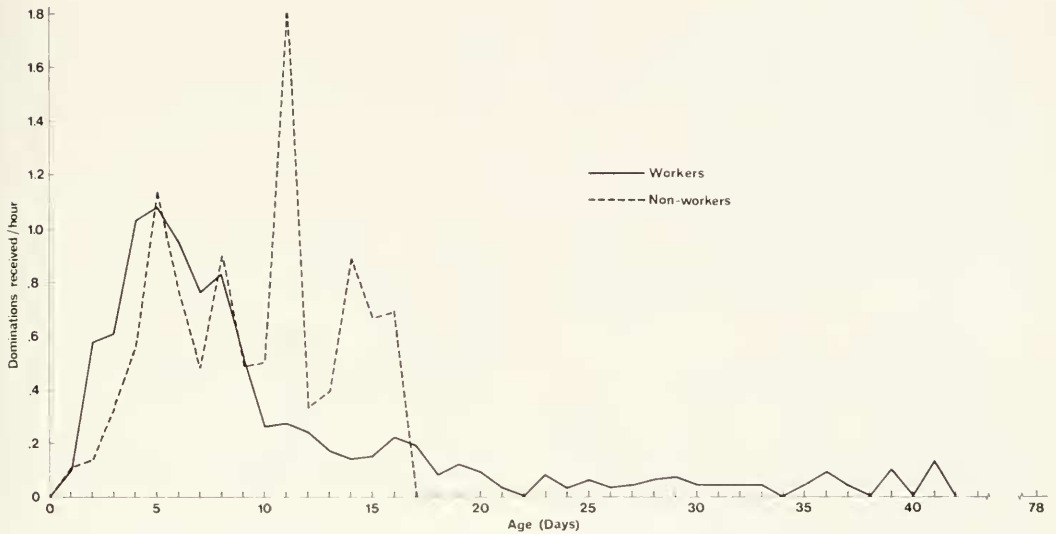


Figure 7. Rate of submission versus age. The ordinate gives the average number of times a wasp of a given age was dominated per hour of observation. Data pooled from three colonies (174, 268, 342).

declined rapidly until about the tenth day. For the next ten days it declined more. As a worker aged, she became markedly less submissive to domination; rather than going into submissive posture she usually merely lowered the head slightly until the dominant wasp stopped its attack, then she immediately resumed whatever task she was doing when the domination began. A similar pattern was followed by nonworkers, except that they underwent a high average rate of domination for as long as they remained on the nest (Fig. 7).

The concentration of the amount of domination received in one part of the life span indicates that dominance behavior is not directed indiscriminately at any nestmate, but that some condition or characteristic of the subordinate perceptible to the dominating wasp both releases the dominant behavior and causes it to be directed at the subordinate. This supports Pardi's (1947) hypothesis that a wasp recognizes certain characteristics of individuals that reflect their social rank relative to itself. Pardi suggested that odor differences (possibly based on slight differences in amount or kind of food received) may provide the

cues, or that signals may be subtle differences in demeanor, perceived visually by the dominating wasp. Pardi appeared to favor olfactory discrimination, at least in part because it complements his idea that the existence of the dominance hierarchy confers a trophic advantage on high-ranking members of the colony. There is as yet no way of distinguishing between these hypotheses; indeed, odor and behavior may both be involved.

Whatever the characteristics of a subordinate wasp that cause it to be dominated by a dominant nestmate, one thing appears clear: these characteristics undergo an ontogenetic development, reaching a maximum at an age of six days in workers and diminishing afterwards. Pardi (1948b) states that ovaries of *P. gallicus* females undergo a development, reaching a maximum at age 15 days (the ascending phase) thereafter regressing in development. Wasps whose ovaries are in the ascending phase dominate those whose ovaries are in the regressing phase. If young females are dominated sufficiently while their ovaries are in the ascending phase, their development is apparently effectively suppressed

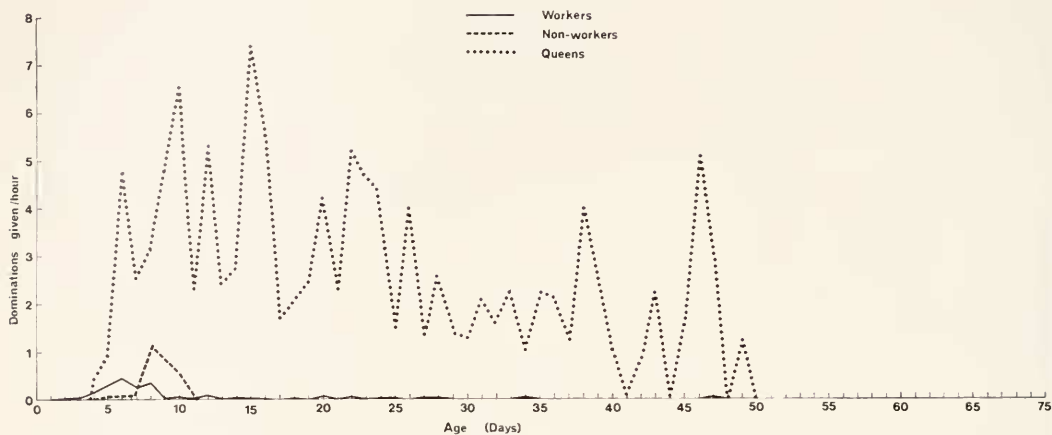


Figure 8. Rate of domination versus age. The ordinate gives the average number of times wasps of a given age dominated nestmates per hour of observation. Data pooled from three colonies (178, 268, 342).

and they become workers. Once their ovarian development is suppressed they apparently require no further domination. Eberhard reached a similar conclusion for *Polistes canadensis*. She suggested "that interactions among adults at the time of emergence or shortly thereafter affect the behavior (caste) of emerging females" (Eberhard, 1969: 71-72). She found that the four females that emerged just before or during a period of conflict following queen removal were nonworkers, but that the next 11, which emerged after the establishment of a new queen, were workers.

The tendency to dominate others also appeared to be greatest among workers around the sixth day of adulthood and to diminish essentially to zero by the tenth day (Fig. 8). The peak for nonworkers came later, on about the eighth day. Queens were most dominant during their earlier days (Fig. 8). Beyond the age of about two weeks their rate of domination gradually diminished.

3. Linear Hierarchy on Established Colonies

Pardi's work with *Polistes gallicus* has shown that a linear dominance hierarchy is established among the female inhabitants of a nest on the basis of the outcome of

dominance interactions between all possible pairs of individuals (Pardi, 1948b). Except for the period just prior to foundation and during the later stages of the colony, when "triangles" occur, the hierarchy is "typically" and "rigorously" linear.

Inasmuch as the outcomes of interactions between a given pair of females are usually the same, i.e., one acts as dominant and the other as subordinate, the same sort of linear hierarchy could be said to exist among the females of a colony of *M. drewseni*. But because workers were not involved in dominance interactions for most of their lives, only a fraction of the female population of a postemergence nest was at any one time involved in dominance interactions. For this reason it is somewhat meaningless to try to determine the strict order of the linear hierarchy among all female offspring. Rather, dominance activity centered among offspring two to ten days old (plus the queen) and hence with time the roster of females involved constantly changed as older ones dropped out and younger ones entered. Thus the role of the "beta" wasp—the most dominant wasp besides the queen—constantly changed hands, passing down the line from older to younger offspring. Instead of moving to the lower end of the dominance scale as

they lost their dominant positions, older females apparently "dropped out" altogether as they assumed worker duties. This dynamic aspect of the linear hierarchy can be seen in Figures 9 and 10.

4. Discussion

The dominance-subordinance interactions described here are similar to those described for *Polistes* (Pardi, 1948b; Morimoto, 1961a, b; Yoshikawa, 1963a; Eberhard, 1969), and apparently function in the same way, namely, to maintain a single egg-laying queen on the nest. Dominance interactions have the effect of conferring upon the queen a trophic advantage while forcing the tasks requiring absence from the nest upon the subordinates; the unequal distribution of food and work, along with the possible direct effects of dominance, results in enhancing ovarian development of the queen while suppressing it in workers (Pardi, 1948b). The workers do not develop to the stage where they challenge the queen in her role of sole egg-layer.

The point brought out by the data presented here is that ovarian development of young females can apparently be suppressed only during a certain critical age, lying in the interval of two to 15 days. This is evidently during the ascending phase of ovarian development. It is during this age that females are dominated most heavily. Once a female has become "worker-ized" she no longer needs to be dominated and is for the most part left alone.

D. QUEEN DETERMINATION ON PRE-EMERGENCE COLONIES

The behavior of subordinates on multiple-foundress pre-emergence nests was more nearly like that of the queen than was the behavior of workers on postemergence nests. This suggests that among co-foundresses of a colony, several or all are fecundated and have the potential of becoming queens and that the one that eventually becomes queen is determined during the

pre-emergence stages of the colony. Pardi (1940) found that all associate foundresses of *P. gallicus* may be fecundated and have developed ovaries, i.e., are "true queens." Rodrigues (1968) found that all the co-foundresses of colonies of *P. versicolor* may be fecundated and have the same degree of ovarian development. Several factors seem to be involved in the establishment of one of them as queen.

1. Dominance, Food Flow, and Work

Pardi (1946, 1948b) and Pardi and Cavalcanti (1951) have shown that enhancement of ovary development is associated with a dominant position, and that regression of ovaries follows a period of subordination to a dominant female. They suggested that the effect is due (in part) to the higher rate of energy consumption in the subordinates on the one hand, and the trophic advantage of high-ranking females on the other. Roubaud (1916) stated that in *Belonogaster* the females that do not forage receive more food and undergo rapid ovarian development, producing ripe eggs by the age of 10–15 days. Females that forage, however, are less well nourished; their ovaries contain eggs, but the ripening of these eggs is delayed as long as they are working as foragers and are poorly fed, even though such females may be fecundated.

The same processes seem to be operating in *M. drewseni*. As was seen (Tables 9 and 10), the queens on pre-emergence multiple-foundress colonies dominated at much higher rates than subordinates. The queen of colony 258 foraged and performed other tasks at low rates compared to her subordinates (Table 5) (though the queen of colony 310 worked harder than her subordinates). The number of times an individual solicited food (nectar and insect) from returning foragers increased with social rank; thus with few exceptions, food passed upward through the social order, from subordinate to dominant (Tables 12 and 13).

TABLE 12. Exchange of foraged food (insects and nectar) between pairs of co-foundresses on colony 258.

Recipient	Donor								Total Received
	66	57	60	54	74	35	16	21	
66		2	4	1	4	1	2		26
57			7	7	2	2	1		19
60	1			2	1	3	3		10
54						6			6
74	1						1		2
35									1
16									0
21									0
Total Given	2	2	12	16	7	18	7	0	64

TABLE 13. Exchange of foraged food (insects and nectar) between pairs of co-foundresses on colony 310.

Recipient	Donor						Total Received
	50	49	57	47	54		
50			16	10	1	1	30
49		1			1		4
57							0
47					1		1
54							0
Total Given	1	16	12	2	4		35

2. Differential Egg-eating

Heldmann (1936), Pardi (1942), Deleurance (1963), Gervet (1964a), and Eberhard (1969) have observed differential egg-eating in *Polistes* and attributed to it an important role in queen determination. Subordinates on multiple-foundress colonies oviposited very infrequently. In 28 hours of observation of colonies 258 and 310 while they were still in the egg substage, on only two occasions were subordinates seen to oviposit (both on 258). Whether these eggs were eaten by the queen was not observed. Observations on 258 were begun four days before the first eclosion; it is possible that in the first few days after founding, oviposition by subordinates was more frequent. In the case of colony 310, though observations were

begun nine days before eclosion of larvae, no subordinate was seen to oviposit. This exclusiveness of the queen in the role of egg-layer was associated with the low level of dominance interactions for that colony. Egg-eating was observed more frequently on 258 after the first larvae eclosed. In five instances eggs of known origin were observed being eaten. In four of these the eggs were eaten by the females that had laid them (the queen on three occasions and no. 57 on one occasion). On the fifth occasion an egg laid by no. 57 was eaten by the queen. Usually when a female ate her own egg she would do so immediately after laying it, suggesting that she was not mistaking her own egg for that of a nestmate. It was not only fresh eggs that were

eaten. In many instances eggs that had gone untouched through several hours of continuous observation were found to have been eaten by the end of the day. Daily records of the contents of brood cells indicate that eggs in all stages of development were eaten. Only ovipositing females ate eggs (queens of 258 and 310, and no. 57 of 258). Oviposition often followed egg-eating, but not necessarily in the same cell.

The egg-eating that occurred after larvae eclosed was probably what is called "nutritional egg-eating" ("oophagie nutritivale") by Gervet (1964a). It will be discussed below (Colony Development, p. 119 ff.). If true differential egg-eating is limited by definition to the egg substage of colony development, the data are insufficient to conclude whether or not it occurs in *M. drowseni*.

3. Empty Cells as Stimuli to Oviposition

According to Deleurance (1950) empty cells stimulate oviposition in *Polistes*. By keeping all cells filled with her own eggs, the queen prevents subordinates from ovipositing (Brian, 1958).

On nests 258 and 310 there were usually one or two empty cells throughout the egg substage of colony development (Figs. 17 and 20). The low rate of oviposition by subordinates on these nests in spite of the presence of empty cells suggests that the queen need not keep all cells filled to prevent subordinates from ovipositing.

4. Age of Co-foundresses

Hamilton (1964a, b) has proposed a genetical theory to account for the sterility of daughter workers on the parental nest. West (1967) has extended this theory to account for the acceptance of nonreproductive roles by the auxiliaries on a pre-emergence nest. According to West, the establishment of a dominance hierarchy among associates serves to maximize k , the fraction by which the addition of each associate enhances the reproductive success of the egg-laying queen. She suggested that

TABLE 14. AGES OF CO-FOUNDRESSES OF COLONY 258 AT TIME OF FOUNDING.

No.	Dominance rank	Age (days)
66	1	10
57	2	14
60	3	14
54	4	21
74	5	1
35	6	36
16	7	46
21	8	52

dominance may act as a "measuring stick" of relative reproductive capacity," by which "siblings sort themselves into groups according to relative reproductive capacity" (West, 1967: 1584).

Evidence from colony 258 suggests that relative age is largely responsible for the initial differences in reproductive capacity among co-foundresses. As was seen in Figure 8, females reached a peak of dominance toward the end of their first week. If their ovaries developed completely they began oviposition by their tenth day (Table 15). After that, their dominance gradually diminished over a period of weeks. Thus, other factors being equal, and ignoring the individual variation that no doubt exists, it could be expected that, of a collection of females of various ages, the one nearest in age to seven to ten days will be most likely to dominate others and become queen. This is apparently what happened among the foundresses of colony 258. The queen was ten days old at the time of founding and the ages of the subordinates increased with their rank in the dominance order (with the exception of no. 74) (Table 14). Numbers 21, 16, and 35, the oldest of the co-foundresses, had actually already been workers on the parental colony and were being dominated very little at the time that colony declined (Fig. 10). Likewise, they hardly participated in dominance interactions on colony 258 (Fig. 10 and Table 9). Numbers 54, 57, and 60,

the next oldest, were nonworkers on nest 174. The oldest of these (no. 54) had been dominated on the parent nest (primarily by the queen, no. 26) and by the time colony 258 was founded her activity in dominance interactions had decreased markedly (Fig. 10 and Table 9). She laid no eggs on 258. Numbers 57 and 60, however, both 14 days old at the time of 258's founding, were apparently young enough still to require dominance. Both these individuals laid eggs on 258 (Table 5) and both were dominated at high rates by no. 66 (Fig. 10 and Table 9). Number 74 was only 1 day old on the date of 258's founding, and no doubt did not join until several days later. Since her ovaries were presumably beginning to develop, she was dominated while on 258 (Table 9).

On colony 310, founded by five females from colony 230, the situation was somewhat different in that the rate of dominance was almost zero and there was no oviposition by subordinates. The queen dominated two of her associates on only three occasions (Table 11). Unfortunately, precise age data are not available, but all co-foundresses had been on the parent nest at least 18 days before 310 was founded, except for no. 57, who had emerged 14 days before 310's founding. Number 50 was the dominant wasp on 230 prior to its decline and was probably the queen. Evidently the dominance hierarchy had been established among the co-foundresses of 310 even before they left the parent nest.

5. Discussion

Flanders (1945, 1946) has proposed that the rate of oviposition may contribute to the determination of caste characteristics as well as sex in the social Hymenoptera, and, more recently (1970), he has argued that adult caste ratios are regulated through the selective cannibalization of caste-biased eggs. According to Flanders, eggs laid at a slow rate lose more of their yolk to ovisorption and do not contain enough nutritive material to produce

queenlike individuals. Wilson (1953) has argued that this hypothesis does not stand up when applied to ants, although Eberhard (1969) admits the possibility that in *Polistes* behavioral differences between worker and nonworker castes may be affected during the egg stage. She points to the concurrent emergence of males and nonworkers in *Polistes fuscatus* colonies and the relationship between oviposition rate and sex ratio as support for this hypothesis.

In *M. dreuseni* the appearance of nonworkers coincided approximately with that of males (Figs. 43, 45, and 46), but there were important exceptions. In particular, the fact that no. 2, the very first offspring to emerge on nest 342, superseded no. 1 as queen argues strongly against any determination of caste characteristics, behavioral or physiological, in the egg or larval stage in this species. In view of this evidence, I think it is quite probable that most, if not all, caste differences between workers and nonworkers in *M. dreuseni* are determined behaviorally in the adult stage. Of course size differences, which may influence behavior in the adult, are determined in the larval stage.

The initial differences in age, hence ovarian development, lead to the establishment of the dominance hierarchy among co-foundresses. This in turn leads to a division of labor, such that those high in the dominance order remain on the nest and perform more of the queen duties, while the lower subordinates forage for food and nest material. The more strenuous work required of foragers and their trophic disadvantage probably are the major factors responsible for the lack of development of their ovaries.

E. QUEEN SUPERSEDURE ON ESTABLISHED COLONIES

The forcible ejection from the nest of the queen by an offspring or younger sibling, who then becomes the new queen, was a fairly regular and apparently normal occurrence. In the course of its entire

development (approximately 160 days) colony 268 had three successive queens. Number 8 superseded her mother, no. 1, and was in turn superseded by no. 36, her sibling. Colony 342 had four queens in its first 155 days. Number 2 took over from no. 1, her mother; no. 10 took over from no. 2, her sibling; and no. 103 took over from no. 10, her mother. On colony 174 no. 1 and no. 26 co-existed on the nest, both laying eggs, for 24 days before no. 26 finally dominated no. 1 and chased her from the nest when the colony was in decline. The succession of queens that took place on colonies 268 and 174 is markedly apparent in Figures 9 and 10, respectively.

Butler (1957) has described queen supersedure in colonies of honeybees. He defined it as "the process by which a colony of honeybees replaces its queen without swarming." Since the same definition can be applied to the process in *M. drowseni*, as described below, use of the same term seems appropriate. The term "usurpation" has been used (for *Polistes*) to denote the process whereby a *foreign* female drives out the queen of a colony of the same species and becomes the new queen (Yoshikawa, 1955). Since the two processes are apparently different, it is probably best to retain the two separate terms.

1. The Nature of Supersedure Behavior

Colony 268 was founded by no. 1 alone. Figure 9 shows dominance interactions beginning on 3 November 1968, the day on which the first two offspring (no. 2 and no. 3) emerged. Thus, the entire period for which dominance activity was possible for no. 1 as a queen is shown in Figure 9. Her rate of domination was quite low; in fact, much of the domination of the first few offspring was done by no. 2 during her first week. After that period no. 1 dominated no. 2 almost exclusively, while no. 2's rare dominations were directed against her younger sisters.

On 30 November no. 8 emerged. She was dominated on her third and fourth

days by no. 1 and by no. 7. By the end of her first week, however, no. 8 had become extremely dominant, directing her attention to her contemporaries, nos. 7, 9, 10, and 11. By 7 December she had begun ovipositing. She did not have any dominance interactions with no. 1 prior to this time; in fact, the two seemed to avoid each other, though when they did come into proximity no. 1 would dart tentatively in no. 8's direction as though torn between a tendency to dominate and a fear of no. 8. Number 8 did not show submissiveness on these occasions. They co-existed in this way until 12 December, when no. 8 began to dominate no. 1 violently. At 4 p.m. no. 8 grappled so violently with no. 1 that the pair fell from the nest. Number 8 returned to the nest immediately, but no. 1 flew to a weed, where she remained for several minutes. By 5 p.m. no. 1 had returned to the nest and was resting in extreme submissive posture while no. 8 rested on the nest face. This was the last time no. 1 was seen on the nest. After this date, no. 8 took over as full-fledged queen, and continued to dominate the younger offspring.

Number 36 emerged on 28 December 1968, and by 3 January 1969, she was beginning to dominate her contemporaries. She in turn was dominated only once by no. 8 and once by no. 33. By 11 January no. 36 was ovipositing, and no. 8 and no. 36 were avoiding each other. After 12 January no. 8 disappeared. I saw no encounter between no. 8 and no. 36, though there may have been one.

By the time observations on the colony ended (18 February) it had begun to appear as if no. 126 may have been about to supersede no. 36 (see Fig. 9). If so, her reign was short-lived, for the colony declined within a week.

2. Age of Superseded Queens

Table 15 gives the histories of founding and superseding queens. Six cases of supersedure were observed. Two additional changes of queens were recorded on colo-

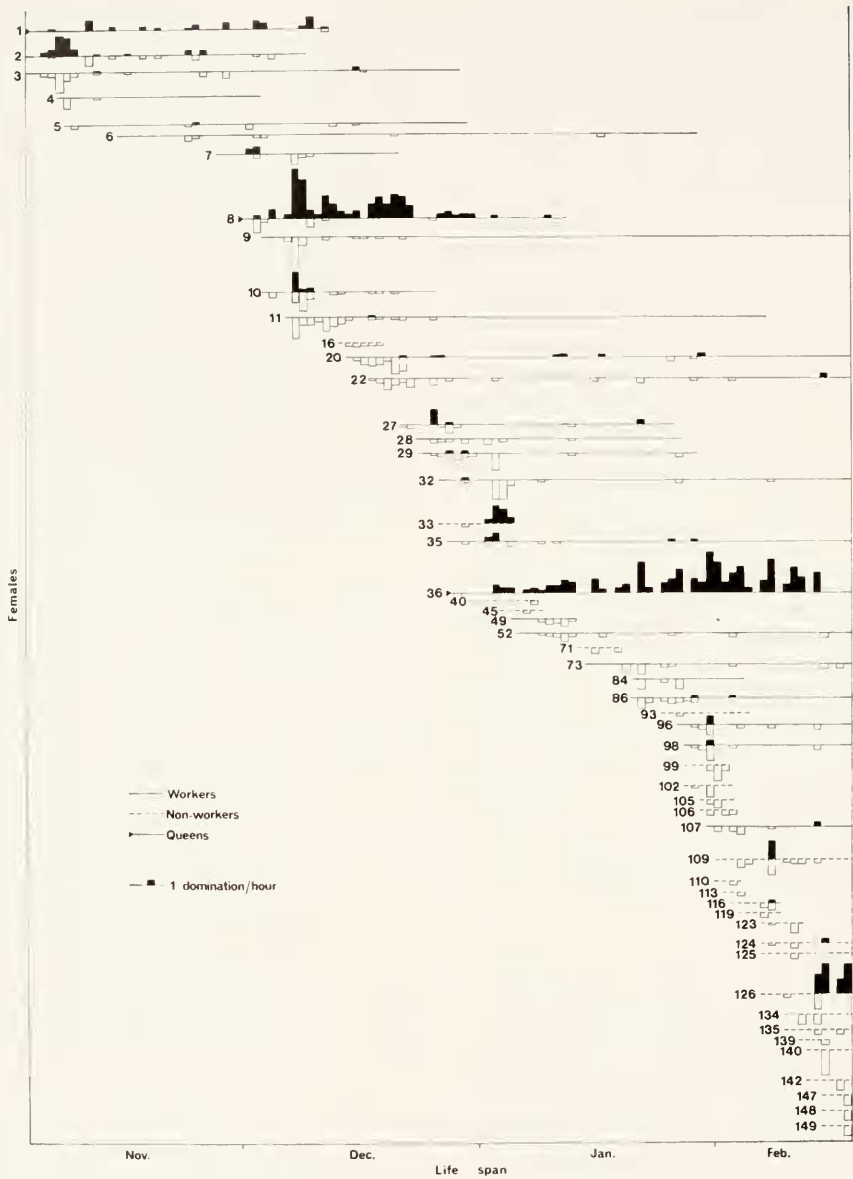


Figure 9. Domination and submission among females of colony 268. Each female is represented by a horizontal line extending from its date of emergence as an adult to its date of disappearance from the nest. The number of each female is given to the left of its line. They are given in order of emergence, from top to bottom. The rate at which each female dominated nestmates is given by a solid bar extending above her line for each day of her life. The rate at which each female was in turn dominated by nestmates is given by an open bar extending below the line. In the rare instances when the observation time was less than an hour, the rate was calculated as if observations had been made for an hour, to reduce unrealistically high rates owing to sampling error.

The 15 females who either disappeared after one day or were not involved in dominance interactions are omitted. Data extend from the emergence of the first female offspring to the end of observations, less than a week before the colony declined.

TABLE 15. Histories of founding and superseding queens. When eggs were first begun late in the development of a colony (168, 174) it was not known whether the queen was the original foundress or a usurper. A + indicates that observations did not bracket the entire life or egg-laying life of a queen. Eggs laid per day was calculated on the basis of the estimate of total eggs laid during egg-laying life made from brood records; this estimate is conservative, since it is likely that many ovipositions were not recorded in brood records.

Colony No.	Queen No.	Foundress or superseding ♀	Relation to ousted queen	Egg-laying life (days)	Life span	Eggs laid per day	Age at first obs. (days)	Age at first observed oviposition	Fate
168	2	?		75+	?	2.6	?	?	observations ended
174	1	?		46+	?	4.	.	.	superseded by no. 26
"	26	S		3.	1	?	.	.	colony declined
231	36	S	?	39+	60	1.6	.	1	colony declined
258	1	F		25+	45	1.9	.	11	observations ended
26	1	F		48	.	2.2	?	?	superseded by no. 8
"	8	S	daughter	36	45	2.2	.	4	superseded by no. 36
"	36	S	sibling	30+	54+	4.4	.	10	observations ended
310	52	F		42+	59+	1.	.	.	disappeared
"	52	S	daughter	6.	??	.	.	.	colony declined
342	1	F		44	.	2.2	.	.	superseded by no. 2
"	2	S	daughter	46	56	2.1	.	11	superseded by no. 10
"	10	S	sibling	60+	60	2.2	18	15	superseded by no. 103
"	103	S	daughter	22+	24	4.2	.	13	observations ended
347	1	F		67+	?	1.7	.	.	observations ended

nies 231 and 310, for which observations were not complete enough to observe how or exactly when the changes occurred. In three of the cases of supersedure the total life span (from emergence to disappearance from the nest) of the ousted queen was recorded exactly. These averaged 60 days (range: 45–79 days). The average active egg-laying life of five ousted queens was 49 days (range: 36–69 days). A sixth ousted queen (no. 1 of colony 174) had an egg-laying life of at least 46 days.

3. Age of Superseding Queens

Table 15 gives the age of each queen at the time she was first observed to dominate a nestmate and to oviposit. The mean age for six queens was five days (range: 3–8 days). Nonqueens (workers and nonworkers), however, were first observed to dominate others at an average age of 8.5 days (range: 4–20) (29 individuals). The age of queens at the first observed oviposition

averaged 10 days (range: 9–15) (7 individuals).

4. Changing Rates of Oviposition

There was no apparent slowdown in rate of oviposition in the colonies toward the end of the egg-laying lives of superseded queens (Figs. 26D, 28D, 30D). In most cases, for a few days before the disappearance of the superseded queen, both old and new queens laid eggs, and during this interval the rate of oviposition of the old queen decreased to zero, but there was no indication that a decreasing rate of oviposition by the old queen might have been the cause of the subsequent supersedure. In the case of colony 174, when no. 26 finally ejected no. 1 she actually oviposited at a much lower rate than did no. 1 prior to supersedure (Fig. 30D), though at this time the colony was well into decline. On colony 342, no. 2 also had a very low initial rate of oviposition.

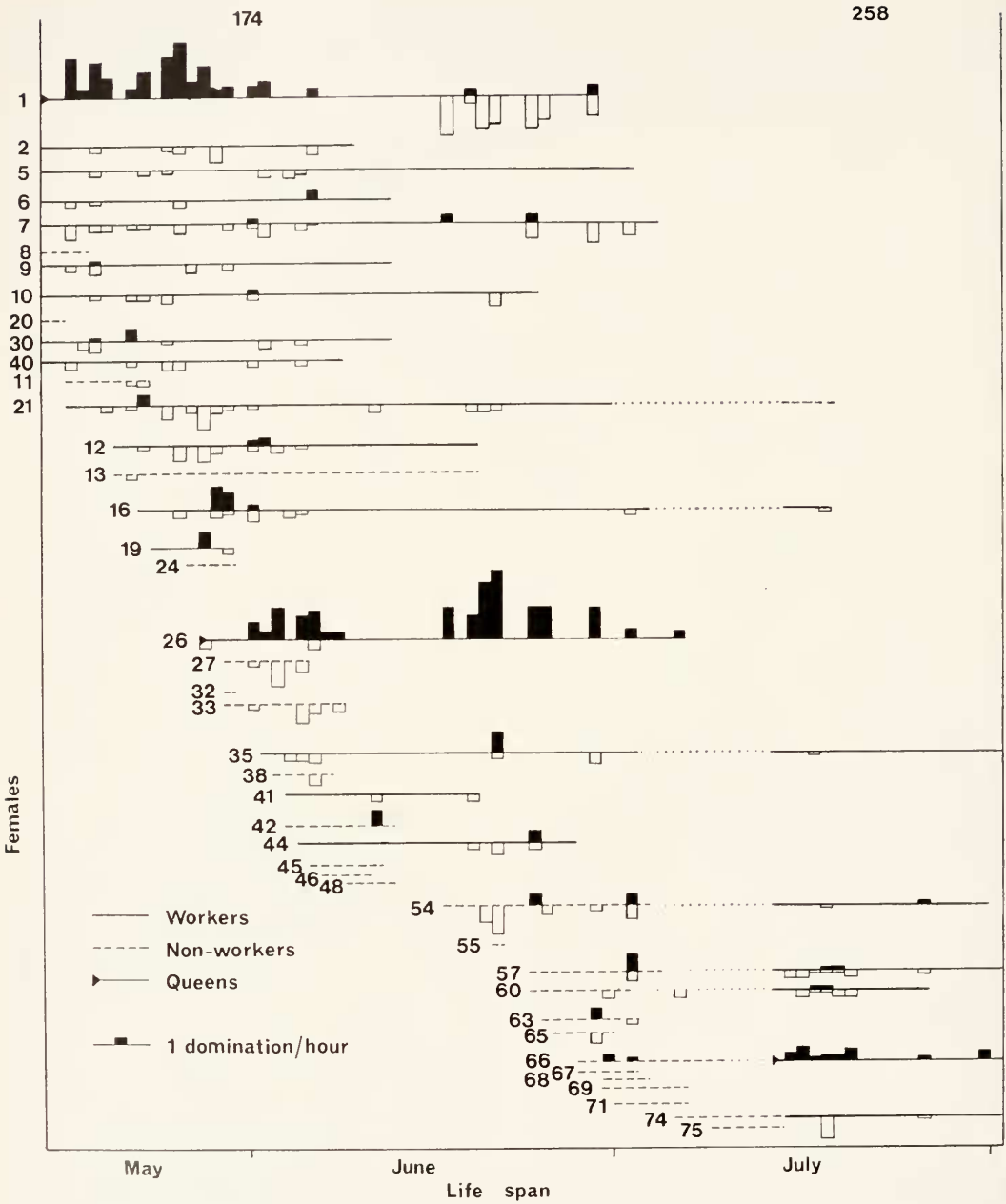


Figure 10. Domination and submission among females of colony 174 and its daughter colony, 258. (See Fig. 9 for explanation of presentation.) Data extend from the postemergence stage through decline of colony 174 and into the pre-emergence stage of colony 258. The interval between the disappearance of a female from colony 174 and its appearance as a co-foundress on 258 is represented by a dotted line.

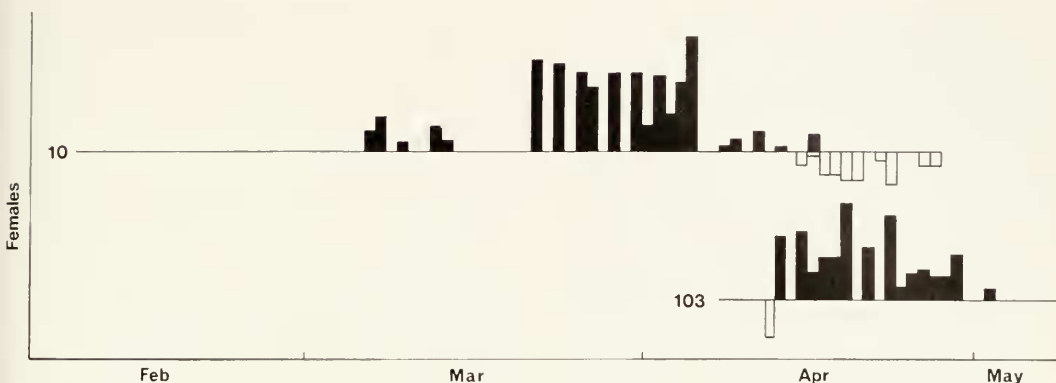


Figure 11. Domination and submission of queens 10 and 103 of colony 342. (See Fig. 9 for explanation of presentation.) The data span the passing of the queenship from 10 to 103.

5. Changing Rates of Domination

In all cases where observations were sufficiently regular to provide data for calculating rates of domination, the superseding queens were dominating at very low rates when they were ejected. This was true of no. 1 and no. 8 on colony 268 (Fig. 9), no. 1 on 174 (Fig. 10), and no. 10 on 342 (Fig. 11). The rate of domination of the superseding queen, on the other hand, was usually high at the time she ejected the old queen. This was especially true of no. 8 on 268 and no. 103 on 342 (Fig. 11), though less true of no. 36 of 268 (Fig. 9) and no. 26 of 174 (Fig. 10). Also, toward the end of a queen's reign, her younger offspring showed more dominance than did those who were young at the beginning of her term. This was especially clear during the reign of no. 8 on 268 and no. 1 on 174 (Figs. 9 and 10).

The rate of domination by no. 1, the foundress of 268, was much lower than that for superseding queens (Fig. 9). By the time she had offspring to dominate, she had put in five weeks of queen and worker duties combined and could well have been exhausted. If this low rate of domination is typical of foundresses, then this is evidence that no. 1 on 174 was not the foundress, since her rate of domination was as high as that for superseding queens

(Fig. 10). Indeed, by the time no. 1 was superseded by no. 26, colony 174 was about 130 days old, much more than the average life span of queens, so it is likely that no. 1 was at least the second queen.

6. Sex of the Offspring of Superseding Queens

Only three superseding queens took over early enough in the cycle of their colonies for their eggs to produce adult offspring. These were no. 8 on 268, and nos. 2 and 10 on 342. In all cases their offspring included females, proof that the superseding queens had been fecundated. Both males and females were among the offspring produced by the first eggs laid by these queens. Number 2 on colony 342 was queen for at least 48 days before any males emerged from the nest, yet the eggs she laid in this period produced adults of both sexes. Therefore, she must have mated with a male from another colony. The nearest known nest containing males at that time was 268, about 30 m away.

The situation that existed on colony 173 presents circumstantial evidence that a superseding queen need not be fecundated. When observations began on 16 May 1968 the colony was approximately 130 days old, yet it had only 38 cells. On that day there were five females and one male on the

nest. Over the next 57 days eggs were laid, the nest grew by cell addition, and then declined. Surprisingly, all of the 25 adults to emerge during this period were males, suggesting that the female who had laid these eggs was not fecundated. The fact that five females were present, though the nest was much older than the maximum age recorded for females, suggests that earlier there had been female offspring and that the original foundress was fecundated. The nest was unusually small for its age (in contrast, colony 174, of approximately the same age, had 115 cells), suggesting that it had undergone a long period of no growth. I suspect that the original queen was lost and there was no fecundated offspring to replace her. Unfortunately, it is not known whether the queen present on the nest during observations was fecundated, for the nest declined before any of her eggs produced adults. It is possible, however, that she was and that nest growth resumed only when she superseded the unfecundated egg-layer or egg-layers.

7. Discussion

As was seen above, the rate at which a queen dominates her nestmates generally decreases as she ages. Therefore, the offspring emerging later in her life as queen receive less domination on the average than those emerging earlier. Apparently, sooner or later one of these offspring does not receive enough domination to cause the inhibition of her ovarian development. As her ovaries develop she becomes increasingly dominant, and by her tenth day begins to oviposit. The old queen and the developing offspring co-exist on the nest for several days, both laying eggs. Eventually the offspring is able to challenge the queen, dominate her, and replace her as queen. Once the queen is superseded she does not merely regress in social status, but disappears from the nest altogether.

There is evidence that the amount of domination an offspring requires to force

it into a worker role varies greatly from one individual to another. Thus, no. 5 and no. 6 on colony 268 both assumed worker duties with a minimum of domination and did not dominate others at all (Fig. 9). This was in contrast to nos. 2 and 3 on the same nest. It may be that successful superseders are particularly robust individuals who happen to be on the scene at the time the reigning queen is weakening. Number 27 may have been a robust individual who challenged no. 8 as queen before no. 8 was sufficiently weak to be overthrown. Number 27 dominated no. 8 once on 25 December 1968, after which no. 8 bounced back and dominated no. 27 into submission (Fig. 9).

An obvious effect of supersedure is to maintain a vigorous, dominant queen in the colony. Though there is no direct evidence that superseded queens have a reduced reproductive capacity, the decreasing rate of dominance may be a sign of impending reproductive slowdown. Or, since domination plays a key role in caste determination and division of labor and is apparently necessary for the maintenance of the colony, the failure of the queen in this role alone may be cause enough for her replacement.

Eberhard (1969) stated that what she termed "queen substitution" may be a common occurrence in *Polistes canadensis* in Colombia. When she removed the queen from an active colony, cell addition stopped, but cell heightening continued during the subsequent period of conflict. When a new queen became established on the colony, cell addition resumed, forming a shelf of shallow cells distinct from the heightened cells initiated by the former queen. Since such "shelves" were common among abandoned nests, she concluded that regeneration of nest growth by "substitute queens" is a common occurrence. This phenomenon differs from queen supersedure in *M. dreuxeni* in that the old queen apparently first disappears, then there is a period of conflict among her

subordinates, during which there is no nest growth. When one of the subordinates is finally established as queen, nest growth resumes. In *M. drowseni* the conflict is directly between the old and the new queens, is very brief (a day or two), and usually has no visible effect on nest growth (though growth stopped temporarily on 26S when no. 36 took over) (Fig. 19).

The existence of queen supersedure in *M. drowseni* poses several questions. First, why has the colony cycle evolved such that it is several times longer than the reproductive cycle of a single queen? The answer to this may lie in a more complete understanding of the relationships of the wasps with their predators. If colonies are subject to a high rate of failure owing to destruction of brood by such predators as army ants, then it may be advantageous to have several short-lived queens that retain enough mobility and behavioral plasticity to begin a new colony at any time (Richards and Richards, 1951).

Another question is what determines whether a dominant young female with developing ovaries supersedes her mother (or older sibling) and stays on the parent nest as queen, or leaves the parent nest and founds a new colony. I suspect that the answer to this lies in an understanding of the colony cycle.

X. LIFE CYCLE OF THE COLONY AND ITS INDIVIDUALS

A. DURATION OF BROOD STAGES

1. Eggs

The phenomenon of egg-eating raises difficulties with attempts to determine the duration of the egg stage. Although accurate daily records were kept of the contents of each brood cell on each observation nest, no adequate method was found to determine with certainty when an egg had been eaten and replaced. The only sure ways of detecting that an egg had been eaten were either to observe the act

itself, or to observe the empty cell before it received a fresh egg. Noting the position of the egg in the cell was partially helpful, but often the new egg would be placed in the same position as the original one. Thus, brood development records often indicated that a given cell contained an egg for several weeks, with no information as to how many separate eggs were involved. Because of such uncertainties, it is not possible to compute average duration of the egg stage with accuracy.

An approximate figure for duration of the egg stage may be provided, however. The first few eggs laid in a newly founded nest, *i.e.*, those that produced the first workers, apparently were never eaten and replaced. I have observed neither such an egg being eaten, nor the cells containing these eggs empty. These eggs all developed within 10–13 days (average: 11.1). It is doubtful that the time of development of eggs varies as much as that of the larvae, since the development of the egg is not dependent upon receipt of food. Temperature probably plays the most important role. Thus, 11 days is probably a reasonably accurate approximation of the average duration of the egg stage.

Eberhard (1969) gave 17.1 days as the mean duration of the egg stage for *Polistes canadensis*, with the extremely wide range of 9–28 days. Isely (1922) gave 10–11 days as the incubation time for first eggs of *P. metricus*, and stated that later eggs do not require significantly longer.

2. Larvae

The problem of the detection of removal and replacement does not arise with larvae or with pupae. The duration of the larval stage varied considerably, depending on the stage of colony development. Figures 12B, 13B, and 14B plot the duration of the larval stage against age of the colony. The first larvae to eclose required the shortest time to develop. The variation in duration of larval stage probably reflects varying rates of feeding at different stages of

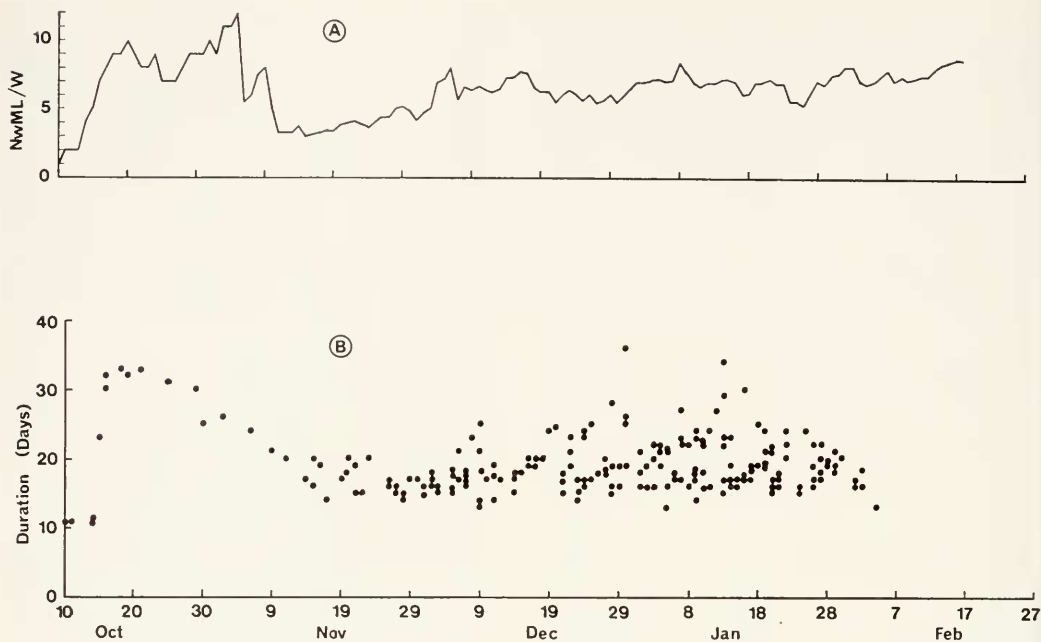


Figure 12. NwML/W ratio and larval duration, colony 268. A. NwML/W ratio. The ratio of nonworkers plus moles plus larvae/workers (ordinate) is plotted against time. B. Duration of the larval stage. Each point represents a single larva. Its date of eclosion is given on the abscissa, and the number of days it required to spin its cocoon is given on the ordinate. Larvae that did not survive to spin are not included.

colony development. This will be discussed further below (Colony Development, p. 119 and following). The minimum developmental time for first larvae was ten days (colony 421), though most required 11–12 days. Following this initial minimum, the curve of larval duration jumped to a maximum of from 30 to 40 days. The maximum recorded time required for a larva to develop was 60 days (colony 354). From this maximum the curve decreased to a second low of around 15 days. Then it rose gradually for the remainder of the colony cycle. The bulk of larvae that eclosed in the postemergence stage of colony development required 15–30 days to develop.

Table 16 gives the average development times for larvae for the entire colony cycle.

The developmental time for larvae of *Polistes canadensis* is 26.6 days (range: 14–53 days) (Eberhard, 1969).

TABLE 16. Duration of brood stages. The average duration of the egg stage was calculated only from the first few eggs laid in newly-founded colonies.

EGGS				
Average: 11.1 days				
LARVAE				
Colony	Average	S. D.	Range	Number
268	19.2	4.4	11–36	205
310	16.3	6.7	11–46	103
342	14.2	6.3	12–46	146
TOTAL	16.2	6.1	11–46	454
PUPAE				
Colony	Mean	S. D.	Range	Number
268	15.0	1.2	12–16	164
310	14.8	0.6	14–16	54
342	14.2	0.5	13–15	129
TOTAL	14.6	0.8	12–16	347

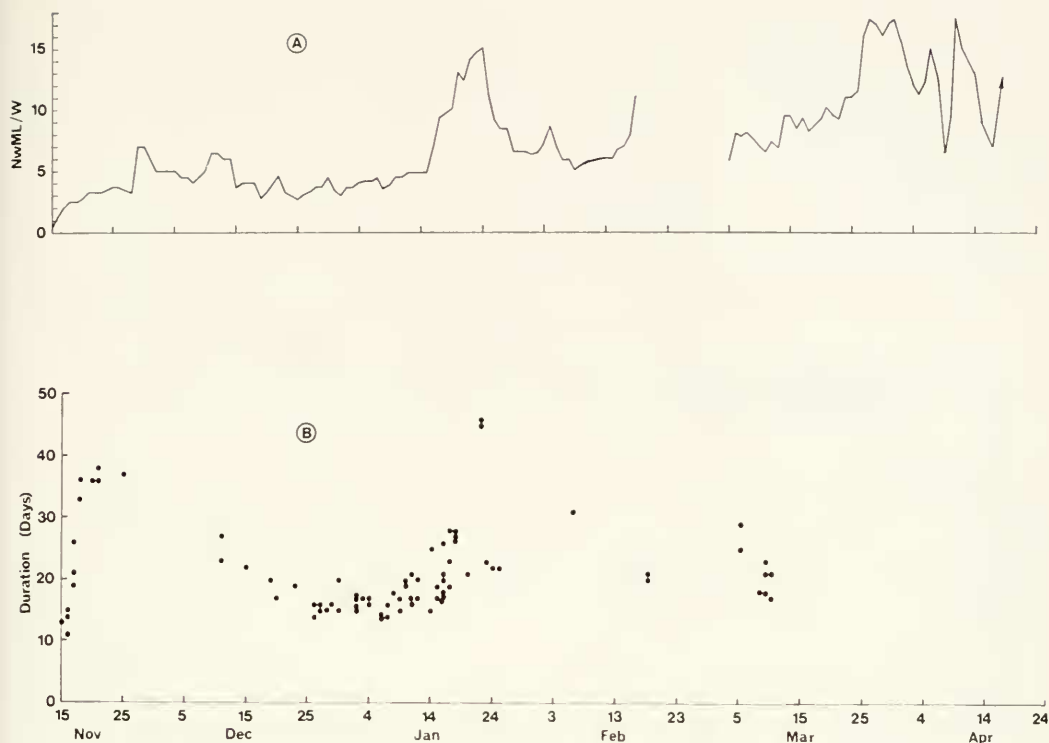


Figure 13. NwML/W ratio and larval duration, colony 310. A. NwML/W ratio. The ratio of nonworkers plus males plus larvae/workers (ordinate) is plotted against time. B. Duration of the larval stage. Each point represents a single larva. Its date of eclosion is given on the abscissa, and the number of days it required to spin its cocoon is given on the ordinate. Larvae that did not survive to spin are not included.

3. Pupae

Duration of the pupal stage varied much less widely than did that of the larval stage. Probably temperature plays an important role in determining rate of development of pupae (Eberhard, 1969). However, in colony 268 the first pupa required only 12 days and the next three only 13 days, while all subsequent pupae required 14–16 days. It was precisely these four individuals whose larval stage was extremely short (Fig. 12B). There was no evidence of a similar shortening of developmental time for the first pupae on either colony 310 or 342.

The overall average time for pupal development for all colonies was 14.8 ± 0.8 days (347 pupae) (Table 16).

There was no significant difference be-

tween the time taken for male pupae and female pupae to develop (71 males, 71 females, 3 degrees of freedom, $\chi^2 = 6.75$, $p > .05$).

Eberhard's data for duration of the pupal stage of *Polistes canadensis* show a much wider variation (7–32 days) than exists in *M. drewseni*. Likewise, Zikán (1951) stated that cells remained covered from 20 to 48 days in *M. scotophilus*. The reasons for this are not apparent. Isely (1922) found that pupae of *P. metricus* in the southeastern United States always required 18 days to develop.

B. SURVIVORSHIP OF ADULTS

Since the date on which each individual emerged as an adult was recorded and daily records were made of its presence on

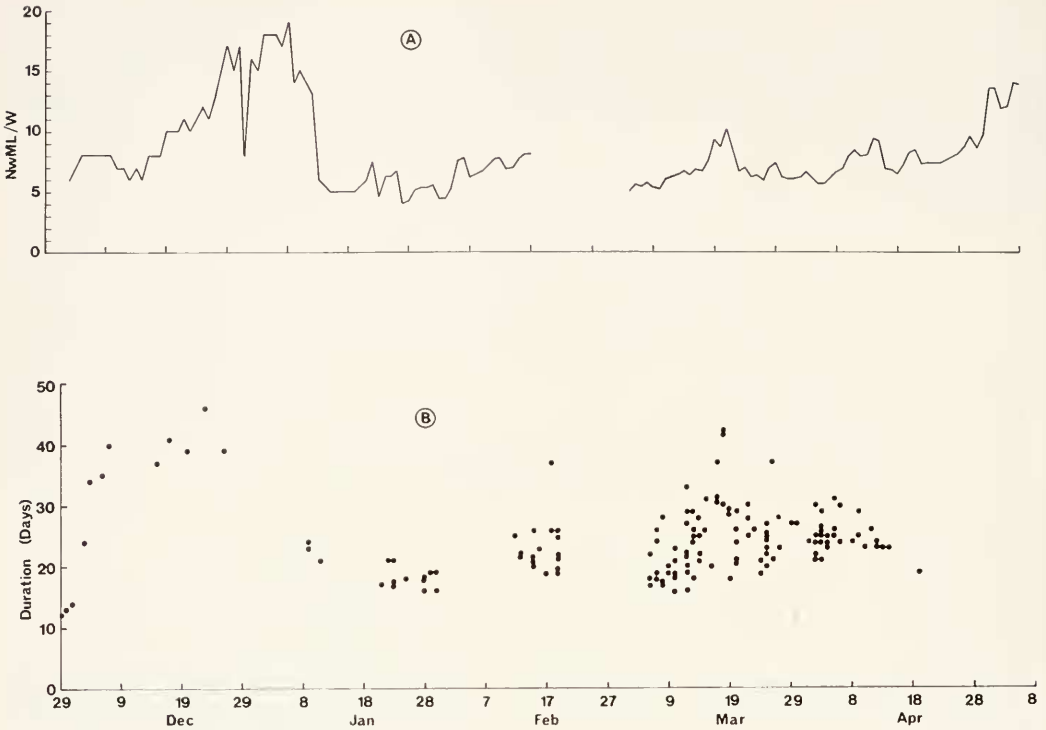


Figure 14. NwML/W ratio and larval duration, colony 342. A. NwML/W ratio. The ratio of nonworkers plus moles plus larvae/workers (ordinate) is plotted against time. B. Duration of the larval stage. Each point represents a single larva. Its date of eclosion is given on the abscissa, and the number of days it required to spin its cocoon is given on the ordinate. Larvae that did not survive to spin are not included.

or absence from the nest, it is possible to construct life tables for the adult wasps. Several assumptions must first be made.

1) The term "life span" as used here is defined as the span of time (in days) an individual is recorded on the nest. Death is probably the reason most workers disappear from the nest, but the same assumption may not be valid for nonworkers and males, since these may leave the nest on mating flights, and some, at least, of the nonworkers may subsequently found new colonies.

2) There were a number of individuals that were not seen on the nest beyond their first or second day. In view of the fact that normally an adult did not leave the nest during its first two to three days, the

causes of such brief life spans are somewhat suspect. It is possible that these wasps were damaged in the process of marking, or by the paint mark itself. Or they may have been sick or weak individuals. Since there are no valid grounds for excluding them from the survivorship data, they are included.

3) Another problem arises with individuals whose entire period on the nest was not observed, either because they had already emerged when observations began or were still on the nest when observations ended. The average life span for such individuals was found not to be significantly different from the average for individuals whose entire life span was known; data from both groups were therefore pooled.

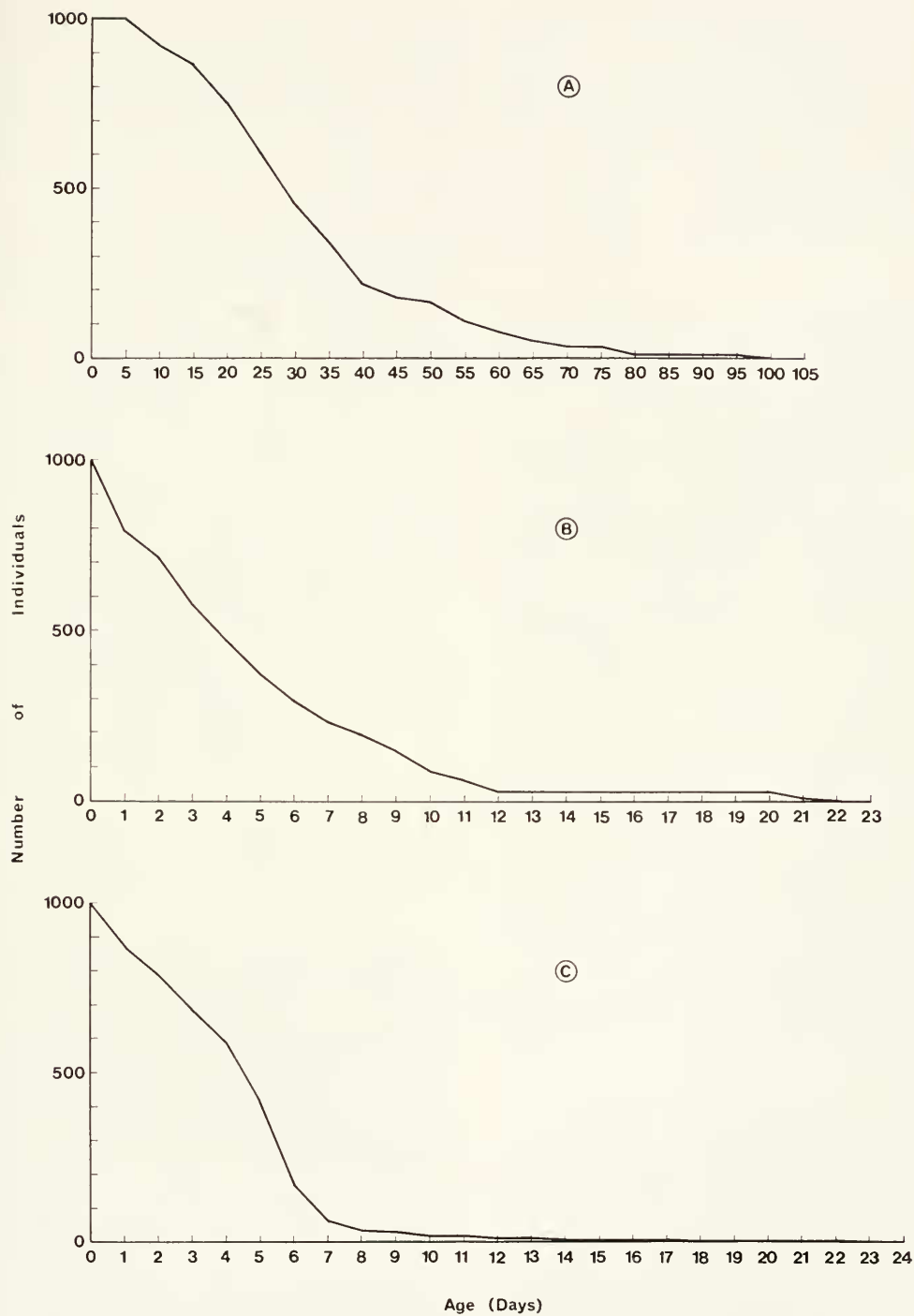


Figure 15. Survivorship of adults. A. Workers (148 individuals). B. Nonworkers (134 individuals). C. Males (323 individuals).

TABLE 17. AVERAGE LIFE SPANS OF ADULTS.

	Average life span (days)	S.D.	Range	No. individuals included
Queens	61	18.7	39-88	6
Workers	31	16.9	6-97	148
Nonworkers	5.0	3.5	1-22	134
Males	4.8	2.6	1-23	323

Survivorship curves for workers, males, and nonworkers (not including queens) are presented in Figure 15. The plateau of 100 percent survival in the first interval of the worker curve (Fig. 15A) is an artifact of the three-day period of "maturation" prior to the development of worker activities. Since for their first three days of adult life wasps remained more or less idle on the nest, it was not possible to determine whether a female was a worker or a nonworker until her third day or so. Thus, all workers had to stay on the nest at least four days, otherwise they could not be identified as workers and were grouped with nonworkers by default. The worker curve approaches Slobodkin's type I (Slobodkin, 1961) for the first 30 days, then approaches type III. Its form is similar to that published for worker honeybees (Sakagami and Fukuda, 1968) except that the change in death rate is not so sudden. The same sort of curve exists for males (Fig. 15C), while the nonworker curve is of type III throughout (Fig. 15B).

Average life spans for queens, workers, nonworkers, and males are presented in Table 17.

C. THE COLONY CYCLE

1. Colony Founding

A new colony may be founded either after the parent colony declines normally, or after it meets with some disaster that the adults escape. As can be seen in Table 18, there was generally a lag of only a few days between the time a foundress left her parent nest and the time she initiated her

own nest, though in one case a colony (353) was founded approximately 25 days before the parent colony (231) declined.

a. *Seasonal asynchrony of colony founding.* Table 18 gives dates of colony foundings for *M. drewseni*, estimated by extrapolation. Though data are not extensive enough to test statistically, there is no suggestion of seasonal synchronization of the colony cycle. The relatively greater number of foundings in the months of February, March, and April is probably attributable to the fact that these months were covered for two years; the low number of foundings in August and September is likewise probably due to there having been no observations during these months. Continuous observations during the course of a year at Taperinha (except for August and September), and spot checks during February, April, and October in Belém, revealed nests in all stages of development in all months. This agrees with Eberhard's conclusion of seasonal asynchrony of colony cycle in *Polistes canadensis* in Cali, Colombia (4°N) (Eberhard, 1969).

b. *Association of foundresses.* Twenty-nine colonies of *M. drewseni* were discovered while still in the pre-emergence stage. Of these, 20 (69 percent) were founded by a single female, 5 (17 percent) by two females, 1 (3.5 percent) by three, 2 (7 percent) by five, and 1 (3.5 percent) by eight. In the four cases where several previously marked females had associated to found a colony (180A, 258, 295 and 310), all co-foundresses on each nest had been marked on the same parent nest; that is, they were siblings. Daughter colonies were always founded within 30 meters of the parent colony, and usually much closer (Table 18).

In no case did I discover a multiple-foundress nest early enough to observe how the co-foundresses came together. I suspect, however, that such nests were initiated by one or two co-foundresses and that the others associated themselves with the venture over the course of several days.

TABLE 18. Estimated dates of founding of colonies of *M. drewseni*. Dates were estimated by extrapolation of pre-emergence colonies based on duration of brood stages. A question mark indicates a colony which declined or was destroyed at about the time the presumed daughter colony was founded nearby, but that the absence of marks on the foundresses of the daughter colony did not permit their positive assignment to that parent colony. Asterisks indicate parent colonies that were destroyed.

Colony number	Estimated date of founding	Parent colony	Date of decline or destruction of parent colony	Approximate distance between parent and daughter nests (m)
168	3 February 1968	-7 days		
173	3 February 1968	-7 "		
174	15 February 1968	-1 "		
180A	27 March 1968	-1 "	18 *	26 March 1969
184	6 April 1968	-3 "		
207	27 May 1968	-1 "		
227	27 June 1968	-2 "		
244	7 July 1968	1 "	174	4 July 1968
268	26 September 1968	-2 "	268*	25 September 1968
269	19 October 1968	- "	264*	14 October 1968
288	3 November 1968	1 "	261	2 November 1968
312	18 November 1968	- "		
347	11 December 1968	- "		
349	8 December 1968	-2 "		
383	12 December 1968	- "	331	7 January 1969
384	11 December 1968	- "		
388	29 December 1968	-3 "		
389	12 January 1969	- "		
421	1 March 1969	1 "	268	1 March 1969
422	18 February 1969	-2 "	268?	1 March 1969
423	18 March 1969	1 "	268?	1 March 1969
424	28 March 1969	-1 "	268?	1 March 1969
425	21 March 1969	-1 "	268?	1 March 1969
426	12 April 1969	-2 "		

The subordinate co-foundresses of a daughter colony were among the last to leave the parent nest, and some were found on both nests for several days during the early stages of the daughter colony. Males, though present on the parent colonies while daughter colonies were being founded, were never seen on the daughter nests.

During the course of pre-emergence colony development, the number of co-foundresses gradually diminished. Colony 258, with a maximum of eight co-foundresses, had only four 24 days after founding. Of the five co-foundresses on colony 310,

only three remained at the emergence of the first offspring. Two weeks later none remained.

2. Colony Development

The progress of colony development from initiation through final decline can be traced in terms of brood population and nest size. When a nest is growing, virtually all cells are filled with brood, and new cells are supplied with eggs within a day or so after they are initiated. Consequently, the rate of addition of new cells is a good indicator of colony growth. When the nest is not being enlarged, the

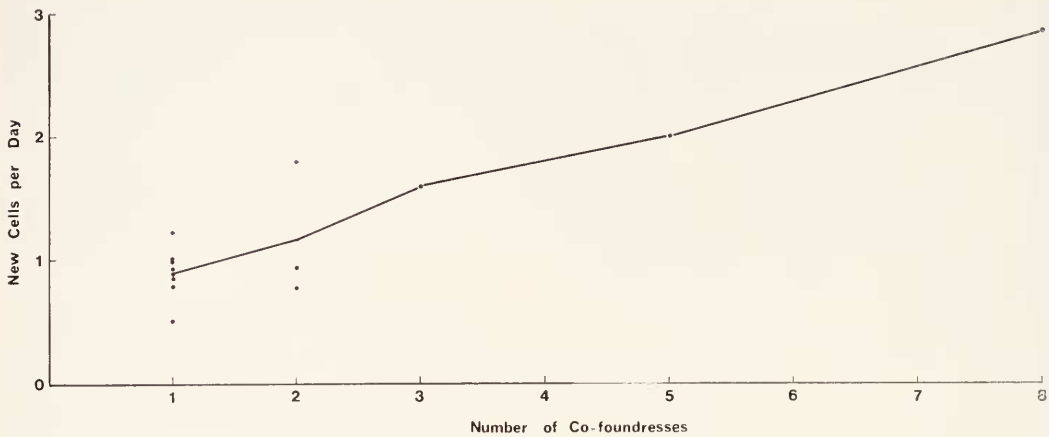


Figure 16. Change in rate of new cell construction with number of co-foundresses. Data are based on rate of nest growth (in new cells per day) before the first larva ecloses. Each dot represents a colony. The line connects average values.

size of the brood population may be either static or decreasing. When the brood is decreasing, cells are emptied of brood faster than they are filled with fresh eggs. Thus, the most convenient indicator of decreasing brood is an increase in the number of empty cells. Cells are emptied of brood in three ways: by the emergence of adults, by egg-eating, and by the abortion of brood. The termination of the colony cycle occurs when the brood decreases to zero and the number of empty cells equals the number of cells in the nest. This was observed in three colonies (173, 174, 310). The progress of colony development is normally one of growth until just before decline, though there may be temporary periods of no growth or even of decrease of brood population at any time. Data pertaining to colony development are most complete for seven colonies. Nest size (in number of cells) and number of empty cells for these colonies are plotted in Figures 17–23. Oviposition rates throughout colony development are presented in Figures 24D through 30D.

a. *The egg substage.* In the period from nest founding until the eclosion of the first larva the queen (or the queen and her co-foundresses) had three tasks: 1) to feed herself, 2) to initiate cells, and 3) to ovi-

posit. As soon as each cell was begun it was generally supplied with an egg, though occasionally a cell was left empty for as long as a day. Nests grew rapidly and steadily at an average rate of about 0.9 cell per day for single-foundress colonies; this rate increased by about 0.25 cell per day for each additional co-foundress (Fig. 16).

b. *The larval substage.* The first eggs took 11 to 12 days to hatch. With the appearance of the first larvae, the queen's duties changed. She ceased building new cells and turned her attention to feeding larvae and heightening the walls of their cells to keep up with their growth. The cessation of nest enlargement resulted in a "plateau" in nest size. The size of the nest at this point averaged 12 cells (range: 7–17) for eight single-foundress nests and increased with the number of co-foundresses (Table 19). The plateau was more distinct for single-foundress nests (Figs. 18 and 21) than for multiple-foundress nests (Figs. 17 and 20). Similar growth arrest occurs in *Polistes chinensis antennalis* in Japan (Morimoto, 1954a, b) and *P. gallicus* in Europe (Gervet, 1964b).

There was a slight decrease in oviposition rate during this substage (Figs. 25D and 27D). This agrees with what Gervet found for *Polistes gallicus* (Gervet,

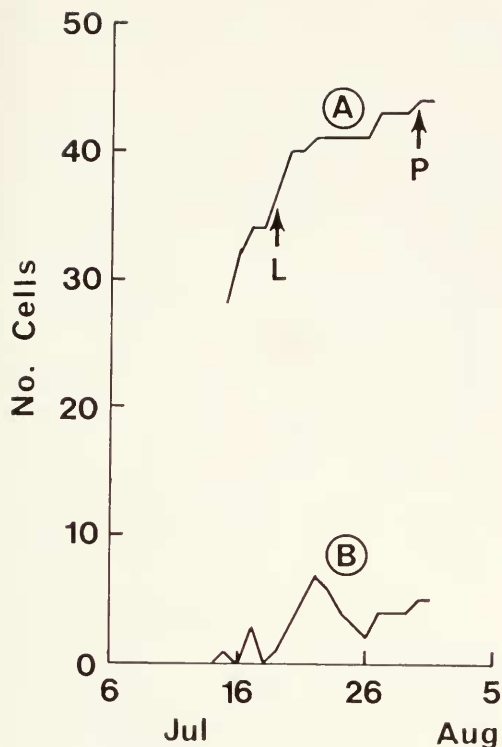


Figure 17. Nest growth, colony 258. A. Nest size in number of cells. L = date first larva eclosed. P = date first larva spun its cocoon. B. Number of empty cells.

1964b), though Morimoto (1954b) reported a complete cessation of egg-laying during the early larval stage in *P. chinensis antennalis*.

After the eclosion of the first larvae several of the eggs in peripheral cells were generally eaten. The rate of egg-eating was highest at the beginning of the larval substage, then tapered off within a few days (Figs. 24C, 25C, 27C). Since the rate of oviposition was reduced below the rate of egg-eating, the net result was a sudden rise in the numbers of empty cells at the beginning of the period (Figs. 17, 18, 20, 21). The number of empty cells then gradually declined as the rate of egg-eating dropped off and the empty cells were filled. This phenomenon occurred in both single- and multiple-foundress colonies. Though the eggs were ingested by

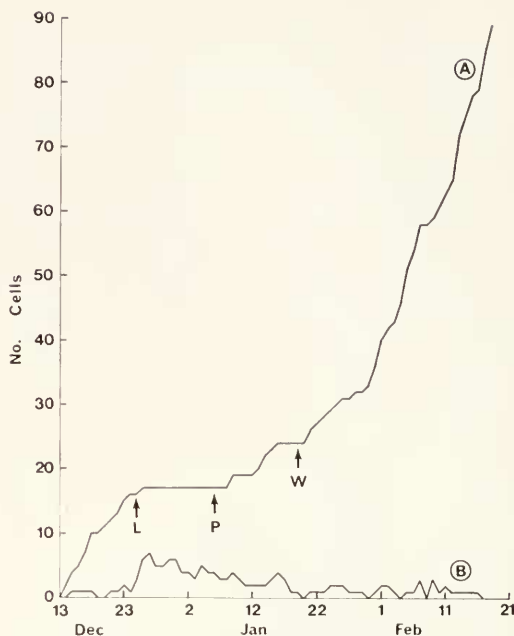


Figure 18. Nest growth, colony 347. A. Nest size in number of cells. L = date first larva eclosed. P = date first larva spun its cocoon. W = date first adult female emerged. B. Number of empty cells.

the oophagic individuals, observation suggests that the egg contents were regurgitated and fed to the larvae, i.e., that they were used as "trophic eggs." Feeding eggs to larvae at this stage in colony development occurs in *P. chinensis antennalis* (Morimoto, 1954c) and in *P. gallicus* (Gervet, 1964a). It is possible that the diet of eggs is responsible for the rapid growth of the first larvae.

There were two other effects of the egg-eating that occurred at this time. First, since nest growth stopped, it enabled the queen to continue ovipositing by making cells available. Second was its effect on the timing of the brood. Since many of the eggs laid just prior to and during the early part of the larval substage were replaced with younger eggs toward the end of this period, the number of larvae in the nest at the beginning of the pupal substage was less than it would have been had the original eggs been left. The consequent lack of

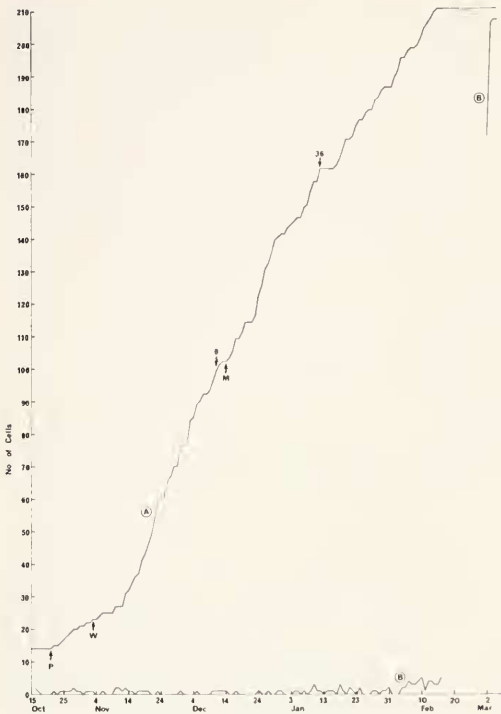


Figure 19. Nest growth, colony 268. A. Nest size in number of cells. P = date first larva spun its cocoon. W = date first adult female emerged. M = date first adult male emerged. 8 = date no. 8 became sole egg-layer. 36 = date no. 36 became sole egg-layer. B. Number of empty cells. Note that this curve continues after the 18 February–4 March break in observations.

eclosing larvae to replace those pupating led to a drop in the number of larvae at this time. This was seen especially clearly in colonies 347 and 310 (Figs. 32 and 34), and less clearly in colonies 268 and 342 (Figs. 33 and 35). The increase in eggs at the end of the larval substage resulted in a rise in number of larvae at about the time the first workers emerged (since eggs and pupae required roughly the same time to develop). Thus the increase in larvae requiring care is neatly synchronized with the increase in the worker force (Figs. 32–35). The drop in the number of pupae, beginning at about the time the first workers emerged, was due to the doubling or tripling of the duration of the larval stage

at this time. This initial periodicity of the brood was damped out completely after workers appeared.

The first two to four larvae to eclose, *i.e.*, those in the central (oldest) cells, grew rapidly, taking only 11–12 days to spin their cocoons (Figs. 12B, 13B, 14B). These formed the first pulse of worker offspring. The number in this first batch averaged 2.6 for single-foundress colonies. In single-foundress colonies the duration of the larval substage of these first workers was distinctly shorter than that for subsequent workers (Figs. 12B and 14B). In the case of multiple-foundress colonies, however, larval duration of the subsequent workers increased more gradually (Fig. 13B). As a result, the first batch of workers on such nests was less distinctly isolated in time of emergence from subsequent workers.

c. *Pupal substage.* Within 22–24 days after nest initiation the oldest larvae spun their cocoons. This, along with the egg-eating during the early larval substage, resulted in a reduction in the number of larvae at this time (Figs. 32, 34).

Beginning at about the time of the first pupation, rate of oviposition rose gradually (Figs. 25D, 26D, 27D). Gervet (1964b) reported a similar rise in *P. gallicus* and Morimoto (1954b) noticed it in *P. chinensis antennalis*. Brian and Brian (1948) noted a similar increase in oviposition rate with the appearance of pupae in *Bombus agrorum* and in *Myrmica laevinodis* and *M. ruginodis*. This rise in oviposition rate was coupled with a drop in the rate of egg-eating, so that cells that were left empty during the larval substage began to fill up.

Among the eggs laid during the pupal substage of colony development were those that gave rise to the first males. This agrees with what is reported for *P. gallicus* (Deleurance, 1948) and *P. canadensis* (Eberhard, 1969). This proves that some, if not all, male-producing eggs are laid by queens.

d. *Emergence of workers.* The first workers emerged 35–41 days after colony



Figure 20. Nest growth, colony 310. A. Nest size in number of cells. L = date first larva eclosed. P = date first larva spun its cocoon. W = date of emergence of first adult female. M = date of emergence of first adult male. B. Number of empty cells.

initiation (Table 19 and Figs. 38–41). As these matured they began to assume worker duties. By this time there was an increase in the number of larvae, as the eggs laid at the beginning of the pupal period began to hatch. With the increase in the number of workers, the rate of nest growth increased (Figs. 18, 19) and the duration of the larval stage began to decrease (Figs. 12B, 13B, 14B). The reason for the gradual decrease is clear: larvae that eclosed early (*i.e.*, just after those comprising the first pulse) had proportionately more of their time on the nest before workers emerged and when rate of feeding was slow. Larvae eclosing later spent a greater proportion of their time as larvae when workers were present and feeding was faster.

e. *Emergence of males and nonworkers.* The first males began to emerge approxi-

mately six weeks after the first larvae pupated (Table 19; Figs. 19, 20, 21). At about this time nonworkers also began to make their appearance. On some nests several nonworkers appeared among the first workers, but these were always individuals who stayed on the nest only one or two days and could well have become workers but for an early disappearance. There was only one exception: no. 9 on colony 310 emerged 10 days before the first male, and stayed on the nest 10 days without being seen to perform worker tasks.

As males and nonworkers appeared and had to be fed by the workers, the rate of nest growth decreased. This was seen in colonies 268, 310, and 342 (Figs. 19, 20, 21). Morimoto (1954a) reported that with the appearance of males, nest growth stops altogether in *Polistes chinensis antennalis*.

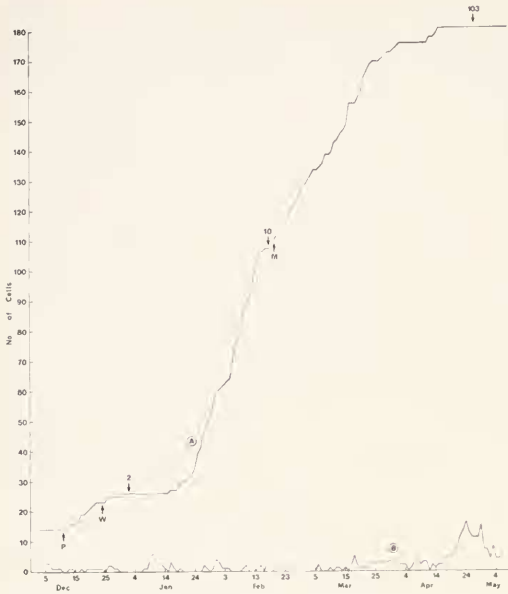


Figure 21. Nest growth, colony 342. A. Nest size in number of cells. P = date first larva spun its cocoon. W = date first adult female emerged. M = date first adult male emerged. 2 = date no. 2 become sole egg-layer. 10 = date no. 10 become sole egg-layer. 103 = date no. 103 become sole egg-layer. B. Number of empty cells.

This occurred only on colony 310 (Fig. 20). There was a gradual increase in average duration of larval stage in the later postemergence period (Figs. 12B, 13B, 14B).

f. *Decline.* After about 10 weeks of male and nonworker production, adults on the nest began to abort the brood, eating larvae and pupae. Brood abortion began with the central cells and progressed outward. Brood was aborted by queens, workers, nonworkers, and males. When pupae were aborted, the caps of their cocoons were chewed away, and the pupae were pulled partway out of their cells and chewed. Smaller larvae were usually completely removed from their cells and chewed up in one piece. Usually several adults shared in the food. Females, after chewing a lump for several minutes, usually fed it to larvae, just as with solid food brought in from the field. Males, after ex-

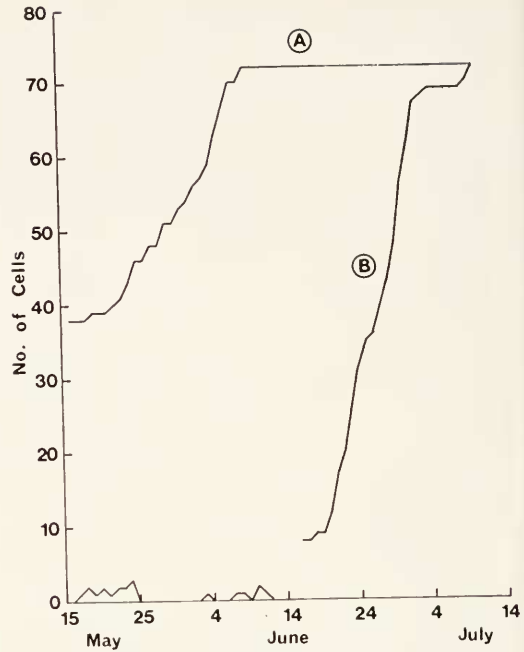


Figure 22. Nest growth, colony 173. A. Nest size in number of cells. B. Number of empty cells.

tracting the juice, either dropped the remainder or passed it on to nestmates or to larvae. The guts of pupae were not eaten.

Queens usually continued to oviposit during decline (Figs. 27D, 29D, 30D), but not rapidly enough to keep cells filled as fast as they were emptied. As the brood decreased, the rate of emergence of adults dropped off; the number of adults (mostly nonworkers and males) on the nest diminished as they left and were not replaced. Ultimately, the brood was reduced virtually to zero, the last adults disappeared, and the colony cycle was complete.

Table 19 summarizes data on size and age of the several colonies at various points in their development. Though the final size of nests varied widely (72–210 cells, 8 colonies), the estimated age of colonies when growth stopped varied much less widely (119–147 days, 5 colonies). Likewise, the estimated ages at final decline showed relatively little variation (145–170 days for 5 colonies). A notable exception

TABLE 19. Colony development data. Age is measured in days from founding. Size is measured in cells. Non-workers include superseding queens. () indicates that an age is estimated (accurate to within 2 days). [] indicates that data for number of adults produced are incomplete because observations did not cover the entire colony cycle.

		Colony Number																		
		223	237	258	295	436	437	493	347	354	421	422	168	173	174	268	310	342	230	231
A.	NO. FOUNDRESSES	2	3	8	2	1	1	1	1	1	2	1	1	1	2	1	5	1		
B.	COLONY DEVELOPMENT																			
	1) Size at first larva	13	22	37	10	7	11	8	17	11	24	13	8			14	24	14		
	2) Size at first worker								24	19	36	14				23	34	23		
	3) Age at first worker								39	(38)	(39)	(37)				(35)	(41)	(36)		
	4) Size at first male															99	75			
	5) Age at first male															(74)	(76)			
	6) Workers before first male															15	13			
	7) Size: termination of growth												>124	72	137	210	114	180	193	118
	8) Age: termination of growth													(125)	(119)	(141)	(147)	(146)		
	9) Age at final decline													(160)	(145)	(160)	(175)	>169		
	10) Days from termination of growth to final decline													33	26	19	29	>23	>21	>194
C.	ADULT PRODUCTION																			
	11) No. workers												(12)	[0]	[6]	[25]	[17]	[43]	[7]	[4]
	12) No. non-workers												(11)	[0]	[25]	[45]	[14]	[21]	[22]	[19]
	13) No. males												(26)	[25]	[30]	[91]	[35]	[110]	[17]	[14]
	14) Total offspring												(49)	[25]	[61]	[161]*	[66]	[174]	[46]	[37]
	15) Males/female: total brood													=		1.30	1.13	1.72		
	16) Males/female: females after first male												1.13		0.97	1.65	1.94	2.62	0.59	0.61
	17) No. adults produced by oldest cells															3	3	3	3	

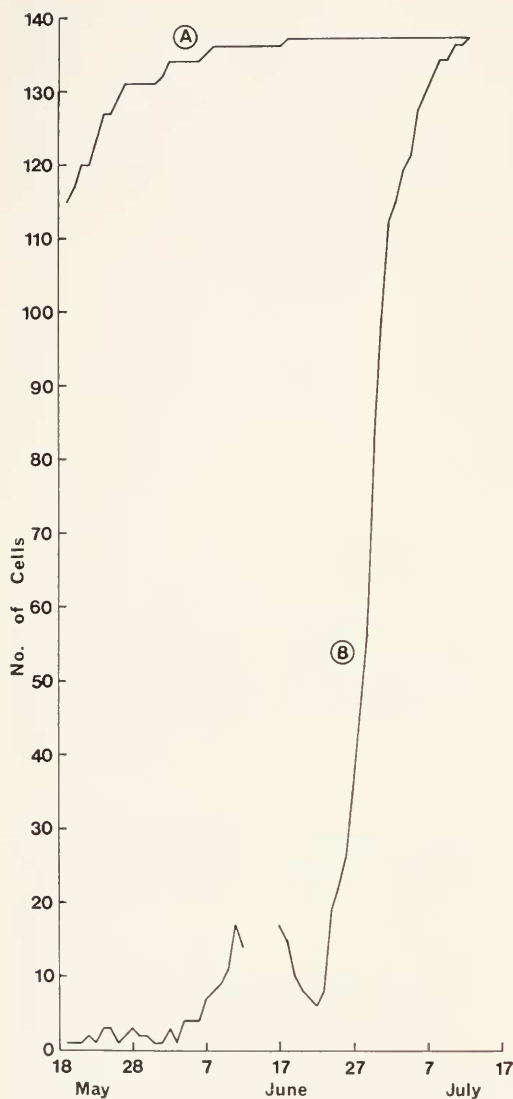


Figure 23. Nest growth, colony 174. A. Nest size in number of cells. B. Number of empty cells.

to this was colony 195 in Belém, which was active for at least 242 days (based on spot checks spanning 242 days).

Unless a colony was observed daily for its entire postemergence development, it was impossible to know the total number of offspring produced. Colony 310 was observed for its entire cycle, but with a

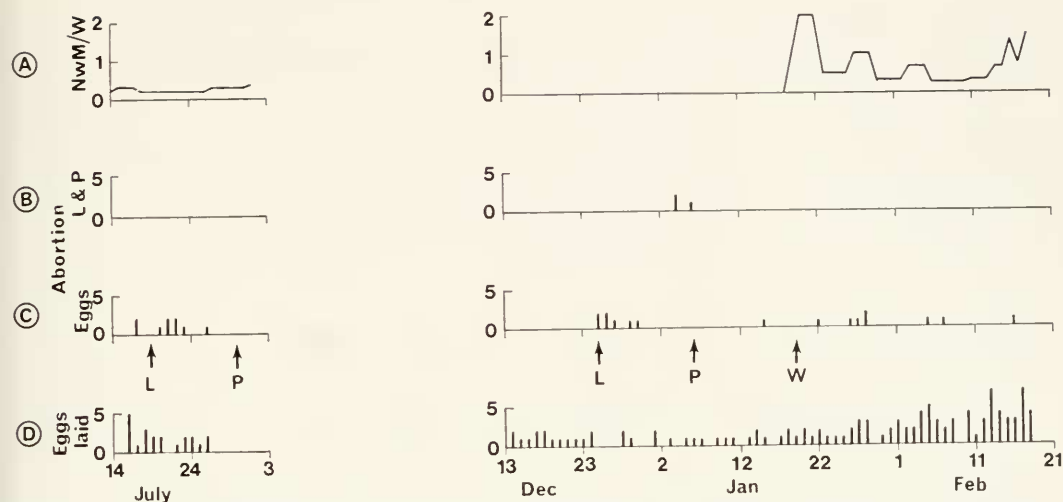
13-day gap during the postemergence period. During this gap 12 cells containing pupae were emptied. If they all produced adults the total production for the colony would have been 78 adults. Colony 268 declined during the same gap in observations. Though some of the 39 pupae present in the nest when observations ended may have been aborted, if they had all produced adults, the total adult production of the colony would have been 200. On the basis of these admittedly limited data, it would appear that the total productivity of a colony (in terms of adult offspring produced) bears little relation either to the number of foundresses or to the length of the colony cycle. It is probably more dependent upon the success with which it produces workers early in the postemergence stage.

No cell was observed to produce more than three adults throughout the entire colony cycle, though many of these contained larvae or even pupae of a fourth generation when the colony declined. This apparent constancy of the number of generations of brood produced by a colony is correlated with the relatively constant duration of colony development.

3. The Regulation of the Colony Cycle

Several attempts have been made to analyze the colony cycles of social wasps. Bodenheimer (1937) reviewed the literature pertaining to this problem. Richards and Richards (1951) have produced a mathematical description of the growth of colonies in terms of workers and brood. Lövgren (1958) has attempted a mathematical prediction of the optimal time for a colony to begin producing sexuals. Brian (1965) discussed a general model that shows the best population size or worker/queen ratio for sexual emission.

Ishay, Bytinski-Salz, and Shulov (1967) have proposed that the series of steps leading to decline of *Vespa orientalis* colonies is initiated by a decline in the supply of



Figures 24 and 25. Fig. 24, left. NwM/W ratio and rates of abortion and oviposition, colony 258. Fig. 25, right. NwM/W ratio and rates of abortion and oviposition, colony 347. A. Ratio of nonworkers plus males/workers (NwM/W). B. Rate of abortion of larvae and pupae (larvae and pupae aborted per day). C. Rate of egg-eating (eggs eaten per day). L = date first larva eclosed. P = date first larva spun its cocoon. W = date first adult female emerged. D. Rate of oviposition (eggs laid per day).

nectar at the end of the season. Their hypothesis is speculative and I shall not go into the details of their argument; suffice it to say that I tend to doubt the validity of any hypothesis that attributes to environmental factors direct roles in the regulation of the colony cycle. In any case such "extrinsic" regulatory factors cannot be invoked to explain the quite regular and delimited cycles of tropical wasps such as *Mischocyttarus*. As has been seen, colonies of *M. drewseni* can be found in all stages of development at all times of the year. The absence of any climatic factors limiting the growth of colonies points necessarily to an intrinsic regulation of the colony cycle. It is probable that in temperate species the only response to environmental limits to growth has been evolutionary, *i.e.*, intrinsic regulatory mechanisms have evolved such that the colony completes its cycle in the time available.

Eberhard (1969) has brought forward evidence that the colony cycle in *Polistes canadensis* and *P. fuscatus* is controlled by the queen's reproductive cycle; she con-

cluded that a reproductively active (ovipositing and cell-initiating) female is required for normal colony development. In colonies she observed, disappearance of the queen or cessation of oviposition was associated with termination of cell addition, and brood decline usually followed.

Several facts suggest that the queen's reproductive cycle does not regulate the entire colony cycle in *M. drewseni*; rather, the state of the colony seems to influence the behavior of the queen to a large degree. These facts are listed below:

a) The fact that a colony normally went through several queens in the course of its development indicates that the colony cycle was relatively independent of the reproductive cycle of the queen.

b) Oviposition rate generally increased with the age of the colony, regardless of the age of the egg-laying female (Figs. 26D, 27D, 28D). The average rate of oviposition of each superseding queen was greater than that of her predecessor (Fig. 42). This suggests that control of oviposition rate lies ultimately with the state

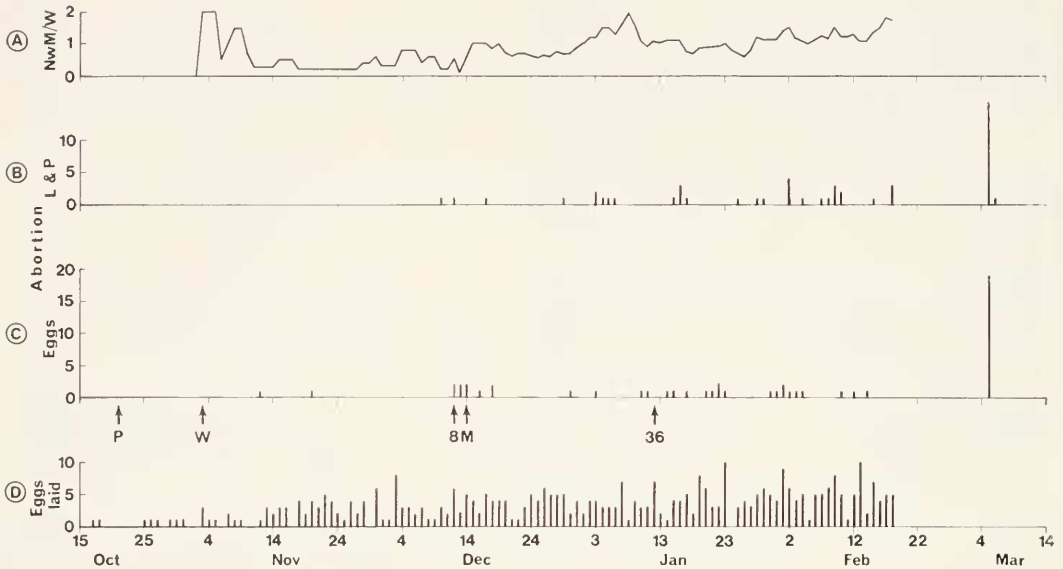


Figure 26. NwM/W ratio and rates of abortion and oviposition, colony 268. A. Ratio of nonworkers plus males/workers (NwM/W). B. Rate of abortion of larvae and pupae (larvae and pupae aborted per day). C. Rate of egg-eating (eggs eaten per day). P = date first larva spun its cocoon. W = date first adult female emerged. M = date first adult male emerged. 8 = date no. 8 became sole egg-layer. 36 = date no. 36 became sole egg-layer. D. Rate of oviposition (eggs laid per day).

of the colony and not with the absolute age or reproductive age of the queen.

c) The deposition of male eggs was dictated by the stage of the colony and not by the age of the queen. Male eggs were not laid before the first brood pupated, *i.e.*, when the founding queen had been laying for about 24 days, but superseding queens laid male and female eggs from the beginning of their reproductive lives, so that there was no interruption in the production of males by the colony.

d) Oviposition by the queens often continued well into colony decline. This suggests that colony decline was independent of the presence of a functioning queen.

e) Colony decline occurred in the presence of a queen of any age. Queen no. 10 had been ovipositing for at least 65 days and was 88 days old when colony 310 declined. At the other extreme, when colony 174 declined, no. 26 had been ovipositing for only 30 days and was only 39 days old. This suggests that the factors

triggering decline were independent of the reproductive age of the queen.

In the light of these facts, it seems impossible to conclude that the development of the colony cycle is solely a function of the queen's reproductive cycle. It is much more plausible that the queen, the workers, and certain properties of the colony as a whole all come into play in an interacting whole (Pardi, 1948a; Michener, 1964). The hypothetical steps in the regulation of colony development are proposed here in outline form and are then discussed.

a) The development of the colony up to the emergence of the first workers is a function of the queen and her responses to the stimuli provided by the state of the colony. Subordinates present on multiple-foundress colonies assume worker roles soon after colony founding.

b) As female offspring begin to appear, the queen dominates them and they assume worker roles, taking over the tasks of feeding the larvae and the queen.

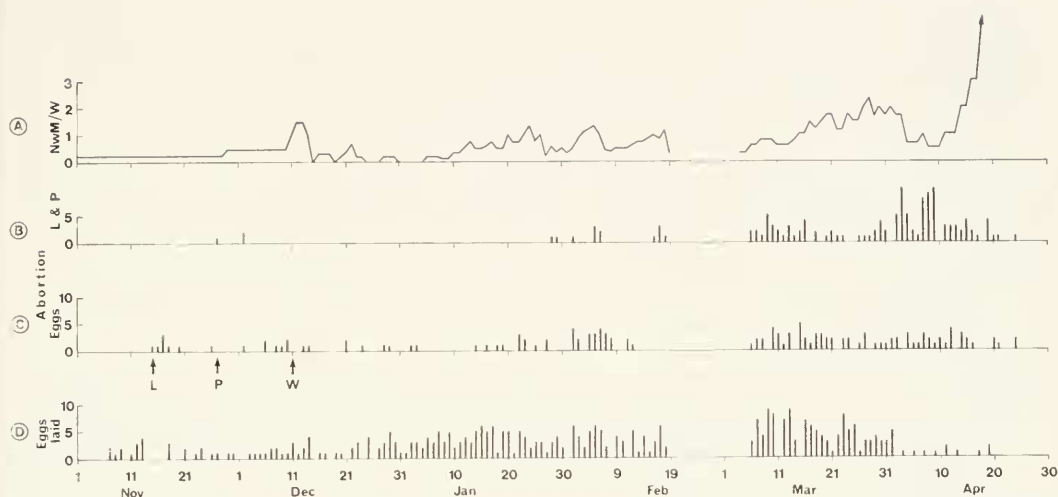


Figure 27. NwM/W ratio and rates of abortion and oviposition, colony 310. A. Ratio of nonworkers plus males/workers (NwM/W). B. Rate of abortion of larvae and pupae (larvae and pupae aborted per day). C. Rate of egg-eating (eggs eaten per day). L = date first larva eclosed. P = date first larva spun its cocoon. W = date first adult female emerged. D. Rate of oviposition (eggs laid per day).

c) As males and nonworkers begin to appear, their demand for food from the workers adds to the tasks the workers must carry out.

d) As the rate of emergence of adults increases with colony age, the amount of domination the queen is able to deliver to each female is reduced. This, along with the larger size of later-emerging females, causes fewer and fewer of the emerging females to assume worker roles.

e) The rapid buildup of nonworkers and males relative to the decreasing rate of replacement of workers results in a rise in the ratio of nonworkers and males to workers (NwM/W).

f) When this ratio reaches a certain point, the workers are no longer able to deliver enough food to the nest to feed the nonworkers and males, and brood (larvae and pupae) are aborted to feed the hungry adults.

g) If the NwM/W ratio remains high enough for long enough, all the brood are aborted, the adults disperse, and the colony declines.

a. *Pre-emergence growth.* The rate of cell initiation and oviposition during the egg substage is probably fixed within certain limits for each species. The size the nest has attained when the first larvae eclose depends upon this rate and upon the duration of the egg stage, which is probably also fixed.

There has been some controversy over whether oviposition rate determines rate of cell construction or vice versa (Deleurance, 1950; Morimoto, 1954b). The conclusion of Pardi (1948b) that "energy consumption dependent on intense work" contributes to the regression of ovaries in workers may be applicable to the queen during the pre-emergence stage, so that the normal reproductive development of the founding queen is regulated by the inhibitory effects of the work she is required to do. During the egg substage the queen has two tasks: (1) to construct new cells and (2) to oviposit. The presence of a ripe egg ready for oviposition may provide the stimulus to construct a new cell if an empty one is not present on the nest. The work involved in foraging for nest material

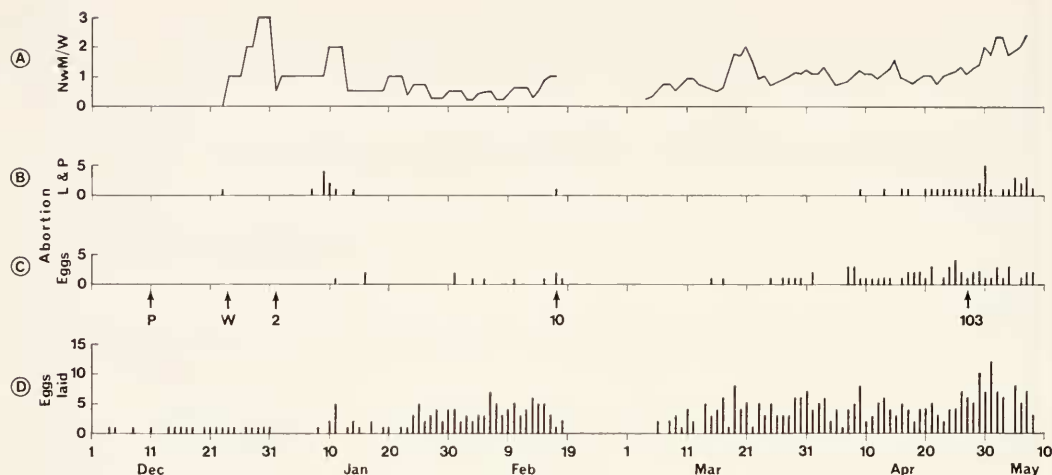


Figure 28. NwM/W ratio and rates of abortion and oviposition, colony 342. A. Ratio of nonworkers plus males/workers (NwM/W). B. Rate of abortion of larvae and pupae (larvae and pupae aborted per day). C. Rate of egg-eating (eggs eaten per day). P = date first larva spun its cocoon. W = date first adult female emerged. 2 = date no. 2 became sole egg-layer. 10 = date no. 10 became sole egg-layer. 103 = date no. 103 became sole egg-layer. D. Rate of oviposition (eggs laid per day).

and constructing such a cell may affect the queen's reproductive physiology in such a way that eggs ripen at a slower rate. Thus, the faster eggs ripen, the more work is required to provide cells for them, and the more work that is done, the slower eggs ripen. This sort of a double feedback mechanism between reproductive physiology and work output is in accord with Pardi's hypothesis.

On multiple-foundress colonies the task of cell initiation is taken over largely by the subordinates. The freeing of the queen from this task, plus the enhancing effects the domination of others has on ovarian development (Pardi, 1948b), could account for the increase in oviposition rate with number of co-foundresses.

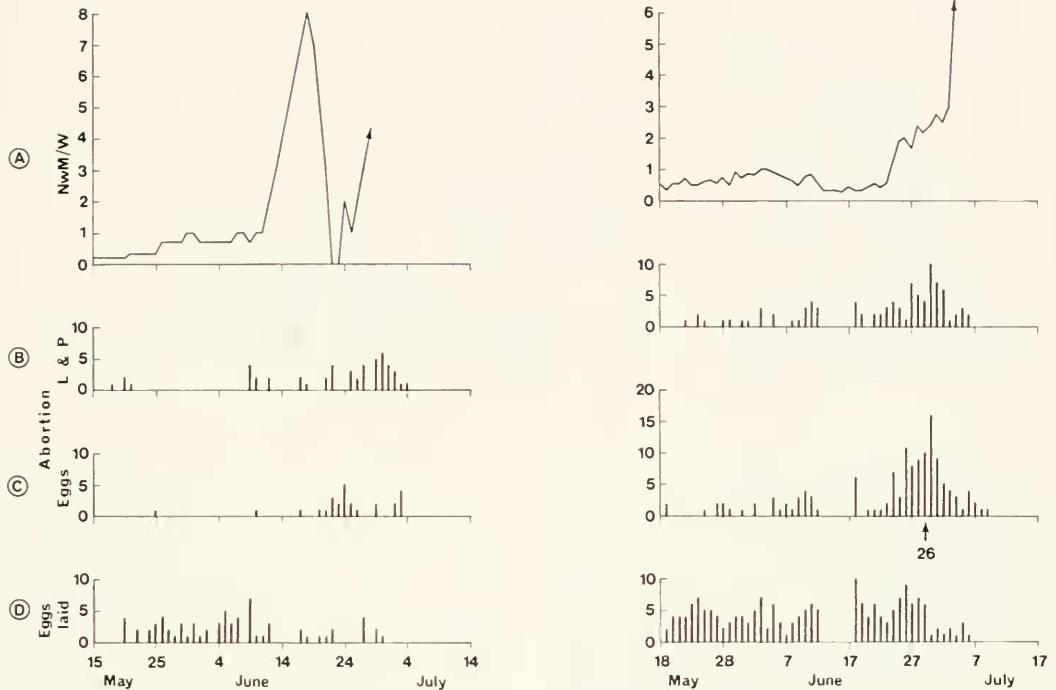
When the first larvae eclose the queen must assume the added tasks of foraging food for them and heightening their cells as they grow. This increase in the amount of work the queen must do could have such an increased "castrating" effect on the queen that her rate of oviposition falls below the rate at which cells are emptied by egg-eating, and no new cells need be

constructed to accommodate the few eggs she lays. In effect, then, the queen becomes more workerlike during the larval substage than during the preceding egg substage.

In multiple-foundress colonies, this "work-erizing" effect on the queen is evidently less severe, since the tasks of feeding and cell heightening are largely taken over by her subordinates. They continue to construct new cells, albeit at a reduced rate, so the rate of nest growth slows during this substage, but does not stop altogether.

Once the first batch of rapidly growing larvae spin their cocoons, the queen apparently feeds the remaining larvae at a much reduced rate, for they develop much more slowly. This reduces her workload, resulting in an increased production of eggs and the resumption of new cell construction. The somewhat slower rate of nest growth during the pupal substage compared to the egg substage suggests that she does devote some energy to feeding the remaining larvae.

In multiple-foundress colonies there is a less distinct separation between the



Figures 29 and 30. Fig. 29, left. NwM/W ratio and rates of abortion and oviposition, colony 173. Fig. 30, right. NwM/W ratio and rates of abortion and oviposition, colony 174. A. Ratio of nonworkers plus males/workers (NwM/W). B. Rate of abortion of larvae and pupae (larvae and pupae aborted per day). C. Rate of egg-eating (eggs eaten per day). 26 = date no. 26 became sole egg-layer. D. Rate of oviposition (eggs laid per day).

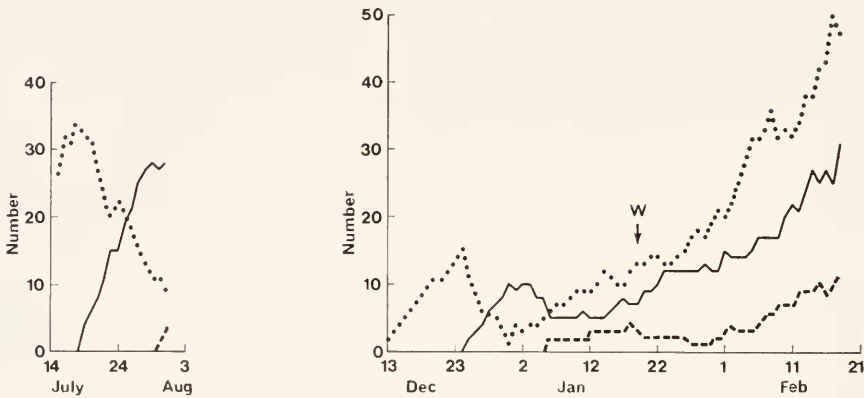
duration of the larvae in the first batch and subsequent larvae, suggesting that the presence of co-foundresses results in a less strict division of tasks among the three substages, resulting in turn in a more even growth of brood population than occurs in single-foundress colonies.

b. *Postemergence growth and decline.* With the appearance of workers, the queen is largely freed from foraging and cell-constructing tasks. Her rate of oviposition increases gradually and the rate of nest growth increases.

Observations suggest that there is a hierarchy of priorities among the tasks the workers must perform in a mature colony. In order of priority, these are: 1) feed the queen, 2) feed the nonworkers and males, 3) feed the larvae, 4) heighten walls of larval cells.

That the queen, males, and nonworkers on the nest have priority over larvae for food is obvious from observation. If food is scarce, returning foragers are mobbed by males and females alike, and all but forced to yield up any nectar or solid food they have. In such situations the larvae get what is left, if any.

How far down the hierarchy of tasks the workers get depends on the balance between food supply (the amount of food the workers are able to bring in from the field) and the demand for food (the number of adults and the number of larvae). It can be assumed for convenience that the amount of food brought in is in direct proportion to the number of workers on the nest. (On single-foundress colonies, the queen is treated as a worker until the first female offspring begin working.) If sup-



Figures 31, 32, 33. Fig. 31, above left. Brood populations, colony 258. Fig. 32, above right. Brood populations, colony 347. Fig. 33, below. Brood populations, colony 268. W = date first adult female emerged. M = date first adult male emerged.

ply is equal to demand, the adults are well fed and the larvae are fed and grow at a moderate rate. If demand surpasses supply, the larvae are first to feel the lack, and reflect it in increased length of the larval

development time. If supply drops still more, and the workers are not able to satisfy even the needs of the adults on the nest, some of the brood are aborted and eaten by the adults, and decline begins.

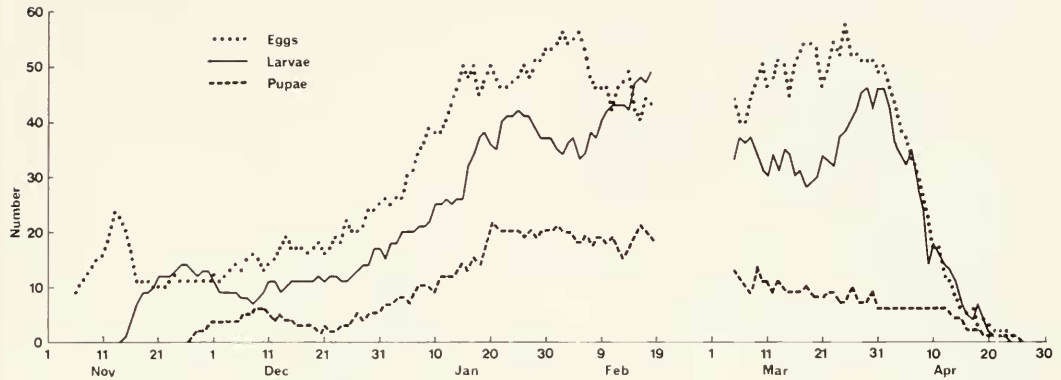


Figure 34. Brood populations, colony 310.

This interpretation of the causes of brood abortion prior to colony decline is in accordance with those of Zikán (1951) for *Mischocyttarus* and Roubaud (1916) for *Belonogaster*. Roubaud found that when mature (foraging) females were removed from a nest, the callows began eating larvae. He concluded that the foragers were necessary for maintenance of the colony and that colony decline was caused by "parasitism" by the abundant males on the mature nest. An experiment performed by Turner (1912) points to the same conclusion. He collected a post-emergence nest of *Polistes pallipes*, leaving the adults behind, and transplanted it to a cage. As offspring emerged he fed them with honey. In spite of these feedings, the adults soon began to eat larvae from the nest. From this point on the adults were provided with insects, and there was no further abortion of the larvae. The larvae were fed by the adults and many pupated and subsequently produced normal adults.

These experiments support the conclusion that brood abortion is initiated when adults are not provided with enough proteinaceous food.

c. *Role of the brood.* The larvae in nests from which the adults were removed survived for more than a week. In times of scarcity the larvae shrank markedly in size and presented a dried appearance. Presumably they maintained themselves at

such times by drawing on their fat reserves. Thus, the larvae can act as a buffer system for the colony during short periods of food shortage, absorbing the stress as an increase in the time spent in the larval stage. Maschwitz (1966a, b) has argued that the larval secretion serves as a "reservoir" of food for the adults during temporary periods of poor foraging. Presumably, even if the adults are not getting enough food via the foragers, they can survive for a short time on larval secretion.

Because the larvae are able to survive long periods without food, it is unlikely that there would be any advantage in reducing the size of the larval population through abortion when the larva/worker (L/W) ratio becomes large. Since the larvae receive food only after the adults are fed, the amount left over for them depends on the nonworker + male + larva/worker (NwML/W) ratio, and of this food allocated to the larvae, the average amount received by each one depends on the L/W ratio. Thus, the combination NwML/W gives an approximation of the average relative amount of food received by each larva. This ratio usually reaches its highest value during the early postemergence period, when there are no nonworkers and males on the nest. Thus, the value of NwML/W at this time is due entirely to



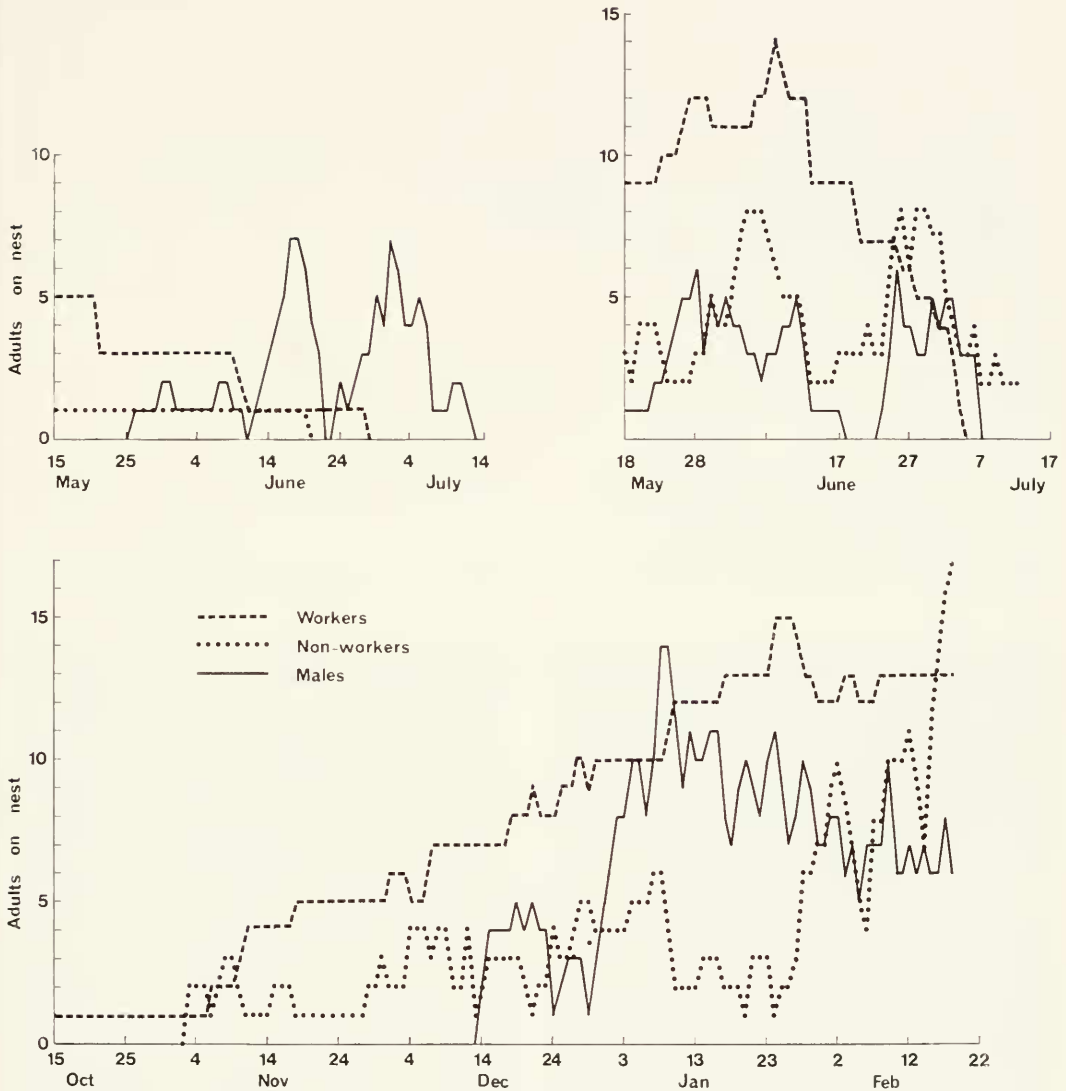
Figure 35. Brood populations, colony 342.

the high number of larvae per worker, yet there is no significant abortion of larvae during this period. (The brood aborted during the larval substage are virtually all eggs, which have no effect on the number of larvae until later.) On the other hand, the correlation between NwM/W and the number of days the larvae spend in the larval stage is quite good, lending support to the proposition that the amount of food the larvae are able to receive affects their rate of growth, but does not cause the workers to regulate larval numbers by abortion when this ratio becomes high (Figs. 12, 13, 14).

d. *Role of the nonworker-male/worker ratio (NwM/W).* Since larvae are fed only after the adults are fed, the amount of food the nonworking adults receive depends on the ratio of nonworkers (Nw) and males (M) to workers (W), and is independent of the number of larvae

present. Figures 36–41 show daily changes in population of workers, nonworkers, and males for six colonies. Figures 25A–30A plot the NwM/W ratios for the same six colonies.

According to the hypothesis, if the NwM/W ratio rises to the point where the workers can just barely feed themselves and the queen, nonworkers, and males, rate of nest growth is zero and the larvae are not fed. An examination of the data suggests that this critical ratio is around 1.4, though this varied from one colony to another. If the NwM/W ratio rises higher than this for more than a few days, the adults begin to go hungry and begin to eat brood. Unless the ratio drops, abortion continues until the brood is reduced essentially to zero, and the colony declines. This is borne out in the correlation between NwM/W ratio, rate of abortion, and the number of empty cells. Colony 174 showed

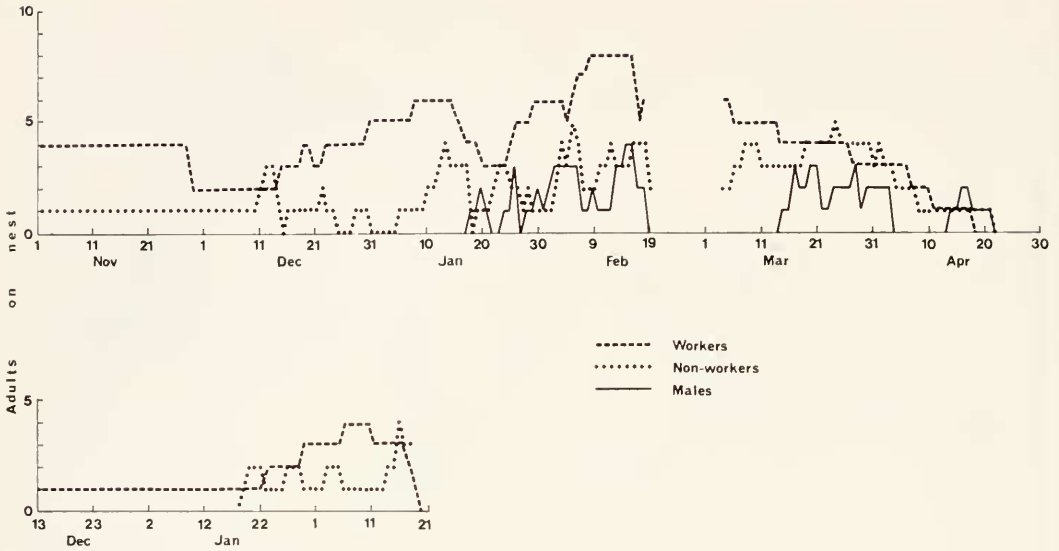


Figures 36, 37, 38. Fig. 36, above left. Adult populations, colony 173. Fig. 37, above right. Adult populations, colony 174. Fig. 38, below. Adult populations, colony 268.

this correlation clearly. During the period from 18 May to 11 June 1968, there was a relatively high NwM/W ratio, reaching 1.0 (Fig. 30A). This was accompanied by a rising rate of abortion of eggs and larvae (Fig. 30B, C) and a rise in the number of empty cells (Fig. 23). Then for the next ten days there was a relatively low NwM/W ratio (about 0.4–0.6) and rate of

abortion dropped below the rate of oviposition and the number of empty cells decreased. Then NwM/W rose sharply, ultimately to infinity as the last worker disappeared (Fig. 37), and during this period abortion rate was very high, causing a rapid emptying of all the cells in the nest (Fig. 23).

Colony 173 also demonstrated this cor-



Figures 39 and 40. Fig. 39, above. Adult populations, colony 310. Fig. 40, below. Adult populations, colony 347.

relation between rise in NwM/W ratio and rise in abortion rate and number of empty cells at colony decline (Figs. 22 and 29).

Colony 310 also showed this, though less well. The increasing NwM/W ratio from 13 March to 3 April 1969 was accompanied by a rise in abortion rate toward the end of this period (Fig. 27). Apparently the low reduction in the ratio from 4 to 13 April was too brief and/or not low enough to have any significant effect on reducing abortion rate, and by 23 April the nest was empty (Fig. 20). The temporary rise in abortion rate and number of empty cells from 4 to 21 March would predict a high NwM/W ratio during the preceding ten days, when no observations were made.

Colony 268 underwent a gradual increase in NwM/W ratio over a period of weeks until 18 February, when a level of 1.8 was reached (Fig. 26A). As of this time there was still no significant increase in abortion rate or number of empty cells, though at this time the nest stopped growing (Fig. 19). During the interval from 18 February to 4 March, when no observations were made, abortion rate increased drastically, so that within a few days after

observations resumed on 4 March, the nest was nearly empty. It is unfortunate that data for this interval are not available.

Colony 342 stopped growing on 16 April, after a period of gradual increase in NwM/W . At about this time abortion of larvae began and gradually increased (Fig. 28). This was correlated with an increase in empty cells (Fig. 21). The subsequent decrease in number of empty cells, despite an increasing NwM/W ratio, seems to have been due to a higher rate of oviposition rather than to a drop in rate of abortion (Fig. 28B, D). The rise in oviposition rate was correlated with the takeover by no. 103 as queen. According to the hypothesis, no. 103 could have prolonged the life of the colony only by increasing the numbers of workers through heavy domination, and not by increasing the rate of oviposition.

e. *The initial high value of NwM/W .* Most colonies showed a high NwM/W ratio when the first offspring emerged (Figs. 25A, 26A, 27A, 28A). This was due to the fact that for their first three days adults did no work and were in effect nonworkers. In calculating NwM/W ratio,

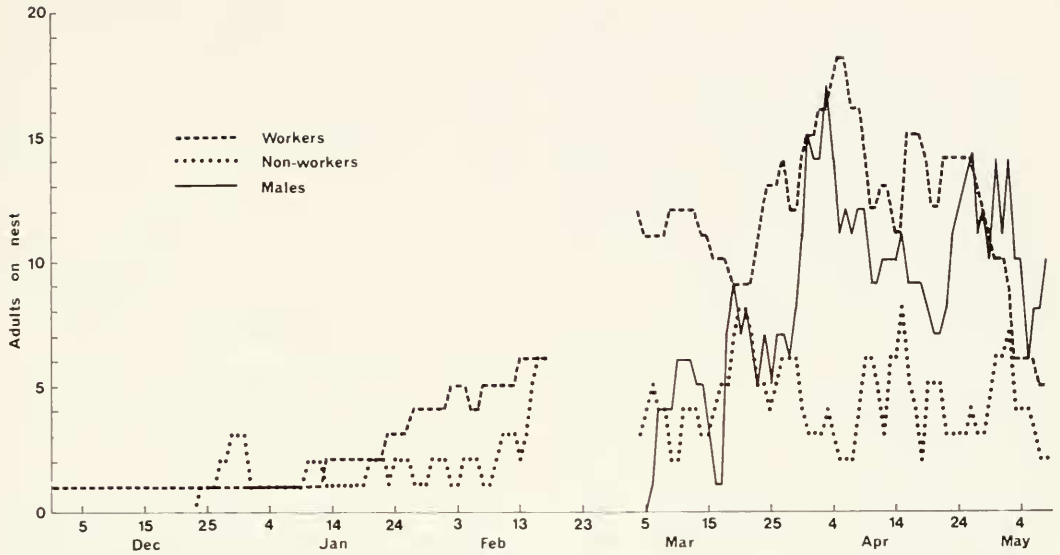


Figure 41. Adult populations, colony 342.

they were counted as such. On colony 268, for instance, NwM/W rose to 2.0 on 3 November 1968, when the first two offspring emerged (Fig. 26A). The queen was still the only "worker" from 3 to 5 November. After three days the ratio dropped then rose again as the next two workers emerged. As the number of workers on the nest increased, the effects of each newly emerging adult on the NwM/W ratio diminished. The same effect was seen in colonies 347 (Fig. 25A) and 310 (Fig. 27A). There was normally no brood abortion accompanying this period of high NwM/W ratio, probably because it was brief and larval secretion could make up for what the queen could not provide.

Colony 342, however, was somewhat unusual in that there was some abortion of larvae (a total of ten) and a rise in empty cells during this period (Fig. 21). This was apparently because the first two adults to emerge were nonworkers. This caused an unusually long period of high NwM/W ratio, long enough for the adults to require more food than the foragers could provide.

The effects of this showed up as a stoppage of nest growth for two weeks, which was unusual for this stage of colony development, and also as a higher peak and more gradual decline of the larval duration curve (Fig. 14B) as compared with those for colonies 268 (Fig. 12B) and 310 (Fig. 13B). This anomaly supports the hypothesis.

Thus there does appear to be a positive correlation between a rise in NwM/W ratio and an increase in abortion. The "critical ratio," or threshold, above which abortion begins probably depends on several factors, which vary from one colony to another. Intuitively, a high ratio would cause abortion to begin within a shorter time than a low ratio.

f. *Factors causing changes in the NwM/W ratio.* There are two immediate causes of change in NwM/W ratio: (1) change in rate of emergence of nonworkers and males relative to rate of emergence of workers, and, (2) since the average life span of workers is six times greater than that of nonworkers and males, a change in the overall emergence rate.

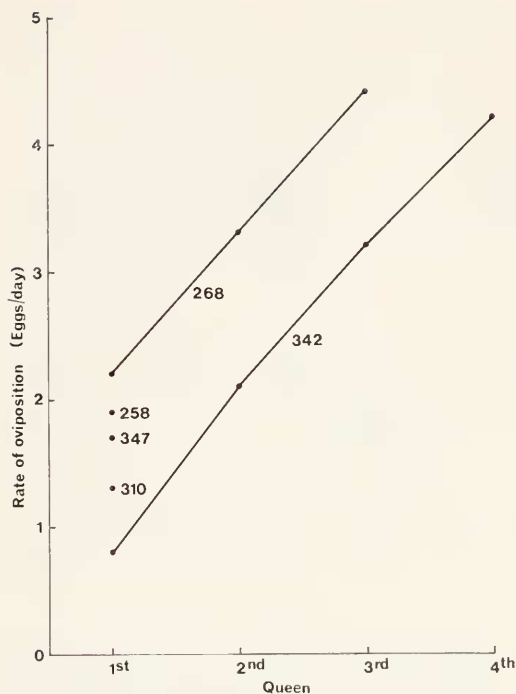


Figure 42. Rates of oviposition of successive queens. Each dot represents a queen. Numbers identify colonies. Abscissa gives the rank of the queen in the series of successive queens for that colony. Thus, "1st" is the foundress, "2nd" is the first superseding queen, etc. Rates of oviposition are estimates calculated by dividing the total observed ovipositions during the reign of a queen by the number of days she was queen.

Colony 268 seems to have been a "healthy" colony, experiencing a smooth growth with no major setbacks. Figure 43 gives the cumulative number of workers, nonworkers, and males to have emerged on this nest against time. Workers began to emerge on 3 November 1968 and continued at a fairly steady rate, averaging 0.2 per day, until 31 January, when the last worker emerged. During the period before any nonworkers or males appeared, the increasing number of workers (Fig. 38) caused a decrease in NwM/W (Fig. 26A).

On 30 November the first nonworker (no. 8) emerged. She challenged no. 1, the founding queen, and on 12 December superseded her as queen. Nonworkers con-

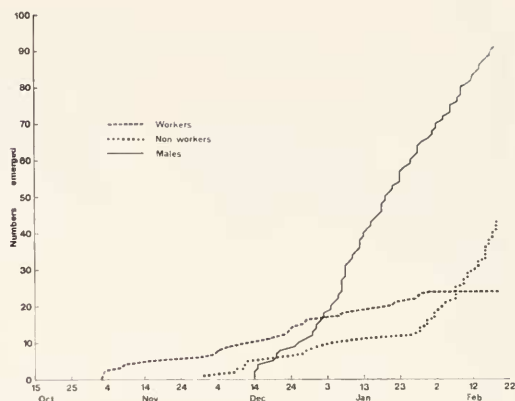


Figure 43. Adult emergence, colony 268. Curves give cumulative numbers of adults emerged.

tinued to emerge at a low rate (0.2 per day) until 25 January. During this same interval males emerged steadily at a rate of about 1.4 per day. Since the combined rate of emergence of nonworkers and males was greater than six times the rate of emergence of workers, the net rate of increase of nonworkers and males was greater (Fig. 38) and NwM/W gradually increased (Fig. 26A).

After 25 January nonworkers began to emerge at the increased rate of almost 1.3 per day (Fig. 43). Males continued to emerge at their high rate. At about this time the number of workers on the nest was at its maximum of 15 (Fig. 38). After 31 January no more workers emerged and their numbers began to decline (Fig. 38), causing the NwM/W ratio to begin to rise at a faster rate than before (Fig. 26A) and the colony to move toward decline (Fig. 19).

The eggs that produced the adults that emerged on 28 January, that is, at the beginning of the upsurge in emergence rate, were laid within a day or two of 12 December, the day no. 8 took over as queen. The rate at which no. 8 laid eggs during the 20 days following 12 December was 3.8 per day, while in the 20 days prior to this date no. 1 had laid only 2.8 per day. This increase corresponds approximately to

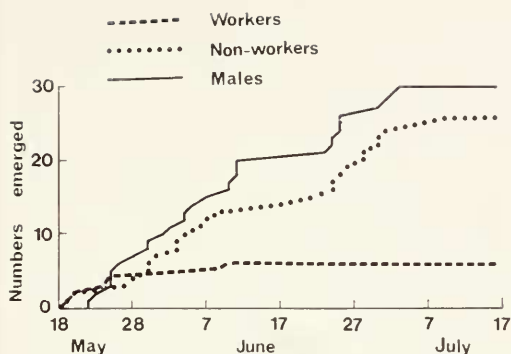


Figure 44. Adult emergence, colony 174. Curves give cumulative numbers of adults emerged.

the increase in rate of emergence ($1.3-0.2 = 1.1$).

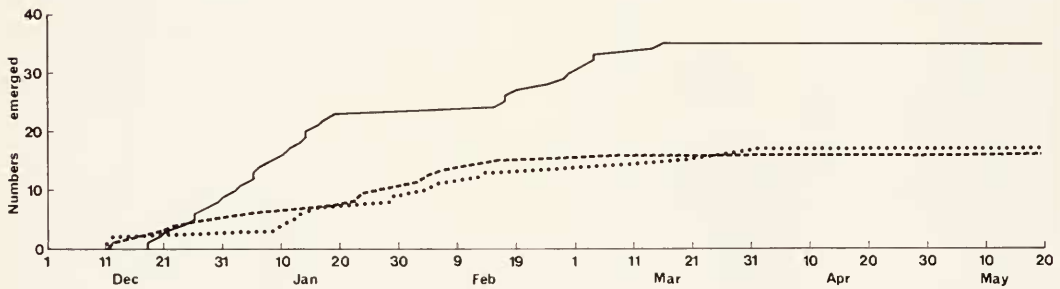
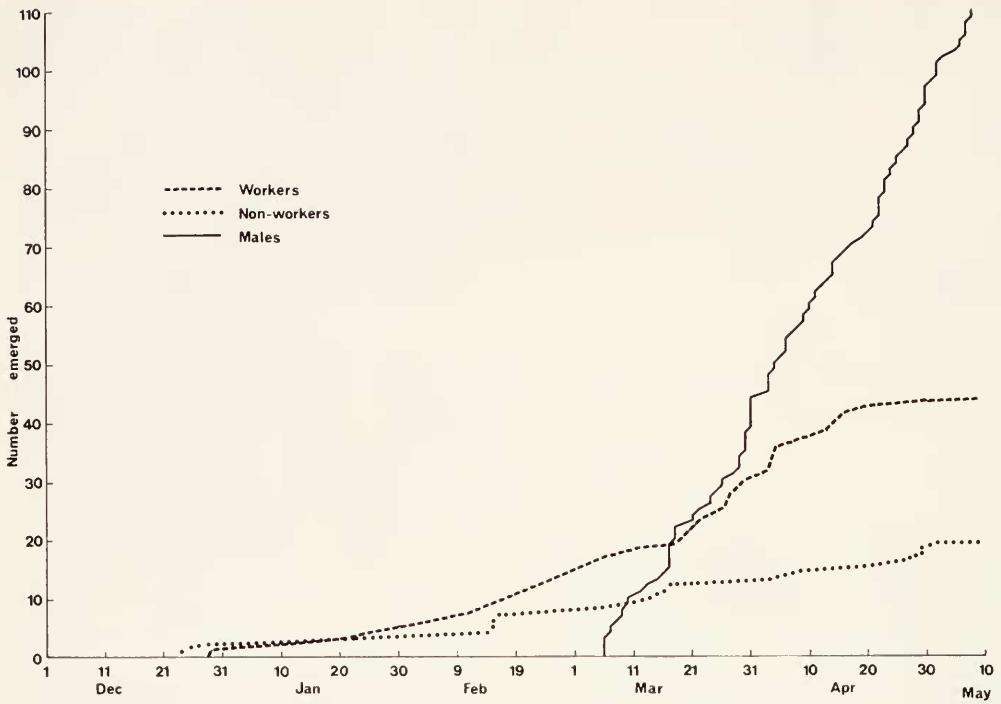
It is interesting that with the change in queens the sex ratio changed. Of the last 50 offspring to develop from eggs unquestionably laid by no. 1, 15 (30 percent) were females and 35 (70 percent) were males. Of the first 50 offspring to arise from eggs unquestionably laid by no. 8, 25 (50 percent) were females and 25 (50 percent) were males. When no. 8 was subsequently replaced by no. 36 on 12 January, she was still producing males and females in a one-to-one ratio.

Colony 174 experienced a rapid rise in males and nonworkers, with relatively little increase in workers through 11 June (Fig. 44). This led to a rise in NwM/W ratio (Fig. 30A) and a slight increase in abortion rate (Fig. 30B, C). But during the next 11 days no males and only two nonworkers emerged, causing NwM/W to drop and abortion to decrease. The number of empty cells diminished, as the cells emptied by the earlier abortion were filled with eggs (Fig. 23). But the respite was short-lived, for the rate of emergence of males and nonworkers rose sharply around 25 June (Fig. 44). Since no new workers were produced, NwM/W ratio rose steeply (Fig. 30A). Rate of abortion again increased (Fig. 30B, C) and this time did not stop until the colony declined.

Colony 342 got off to a slow start because the first two offspring were not workers. The first (no. 2) superseded no. 1 as queen, and the second (no. 3) disappeared after five days. Workers were produced at a low rate (about 0.25 per day) until 19 March. Nonworkers emerged at an even lower rate (0.15 per day). After 19 March workers emerged at an increased rate of about 1.0 per day for about two weeks, then levelled off (Fig. 45). This increase in the number of workers (Fig. 41) caused a reduction in NwM/W ratio (Fig. 28A). The increase in workers seems to have been at the expense of nonworkers; that is, though the rate of emergence of female offspring remained more or less constant during this period, a greater proportion of them became workers. This was correlated with a period of heavy dominance by no. 10, the queen. This lends support to Pardi's hypothesis of psychophysiological caste determination. Sex ratio of emerging adults was 42 (28 percent) males to 110 (72 percent) females during the period of male emergence.

The low rate of nonworker emergence during the period of 19 February to 4 March, when no observations were made, is probably an artifact. Since the average life span of nonworkers was only five days, most of those to emerge in this interval would have been gone before they could have been counted on 4 March. This effect would not be as marked among workers, whose average life span was 30 days.

Colony 310 also experienced a slow initial development (Fig. 20). Again, the first two offspring did not remain on the nest long enough to become workers (Fig. 39). Workers were produced at a rate of about 0.23 per day until 16 February, after which only one emerged (Fig. 46). This was comparable to the rate of worker emergence in colonies 268 and 342. Nonworker emergence rate, at about 0.20, was also comparable to that of these colonies. However, the rate of male emergence, at 0.7 per day, was considerably lower than



Figures 45 and 46. Fig. 45, above. Adult emergence, colony 342. Fig. 46, below. Adult emergence, colony 310. Curves give cumulative numbers of adults emerged.

those for the other colonies. The sex ratio was 10 (31 percent) females to 22 (69 percent) males during the 32-day period from beginning of male emergence until observations ended on 18 February. This was close to the ratio observed during the first part of colony 268's postmale emergence.

Again, the flat portion of the male and nonworker curves in the interval from 19 February to 4 March is probably an arti-

fact of the lack of observations during that period (Fig. 46).

The low rates of emergence of nonworkers and males throughout colony development apparently kept NwM/W high enough to limit nest growth, but too low to cause decline until the ratio was finally raised by the reduction in the number of workers (Fig. 27A).

Colony 173 produced only males during

the period of observation. The only females on the nest were the queen and five workers, already present when observations began (Fig. 36). The possible origin of such a situation is discussed above (Sex of the offspring of superseding queens, p. 111). As workers died off and were not replaced, NwM/W ratio increased (Fig. 29A). The nest contained only 72 cells when growth stopped. Despite the small size of the nest, and the presence of an ovipositing queen, the colony declined when NwM/W became high.

Thus the data presented here, though extremely limited, can reasonably be interpreted to support the proposed hypothesis. Much more data of this sort are needed to confirm the validity of the hypothesis.

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R. L. Jeanne, Chemical defense of brood by a social wasp. *Science*, 168: 1465-1466, 19 June 1970. Copyright 1970 by the American Association for the Advancement of Science. Plate IV, fig. 7.

LIST OF REFERENCES

- ALVAREZ DEL TORO, M. 1950. A summer tanager, *Piranga rubra*, annihilates a wasp nest. *Auk*, **67**: 397.
- BEQUAERT, J. C. 1933. The Nearctic social wasps of the subfamily Polybiinae (Hymenoptera, Vespidae). *Entomologica Am.*, **13**(3): 87-150.
- BERTONI, A. DE W. 1911. Contribución á la biología de las avispas y abejas del Paraguay (Hymenoptera). *An. Mus. nac. Hist. nat. Buenos Aires*, **15**: 97-146.
- BODENHEIMER, F. S. 1937. Population problems of social insects. *Biol. Rev.*, **12**(4): 393-430.
- BRIAN, M. V., AND A. D. BRIAN. 1948. Regulation of oviposition in social Hymenoptera. *Proc. 10th Int. Congr. Ent.*, **2**: 497-502.
- . 1965. Caste differentiation in social insects. *Symp. zool. Soc. London*, **14**: 13-38.
- BRIAN, M. V., AND A. D. BRIAN. 1948. Regulation of oviposition in social Hymenoptera. *Nature (London)*, **161**(4100): 854.
- BUTLER, C. G. 1957. The process of queen super-
sedure in colonies of honeybees (*Apis mellifera* Linn.). *Insectes Soc.*, **4**(3): 211-223.
- DELEURANCE, E. P. 1948. Sur le cycle biologique de *Polistes* (Hyménoptères, Vespides). *C. r. hebd. Séanc. Acad. Sci. Paris*, **226**: 601-603.
- . 1950. Sur le mécanisme de la monogynie fonctionnelle chez les *Polistes* (Hyménoptères, Vespides). *C. r. hebd. Séanc. Acad. Sci. Paris*, **230**: 782-784.
- . 1957. Contribution à l'étude biologique des *Polistes*. I. L'activité de construction. *Annls Sci. nat. Zool.*, **19**(11): 91-222.
- . 1963. Sur le mécanisme de l'oophagie différentielle chez la guêpe, *Polistes gallicus* L. (Hyménoptère, Vespide). *C. r. hebd. Séanc. Acad. Sci. Paris*, **257**: 2339-2340.
- DUCKE, A. 1905. Sobre as vespidas sociaes do Pará. (1^o. Suplemento). *Bolm. Mus. para. "Emilio Goeldi,"* **4**: 652-698.
- . 1907. Novas contribuições para o conhecimento das vespas (Vespidae sociaes) da região neotropical. *Bolm. Mus. para. "Emilio Goeldi,"* **5**: 152-199.
- . 1910. Révision des guêpes sociales polygames d'Amérique. *Ann. Mus. nat. Hungarici*, **8**: 449-544.
- . 1914. Über Phylogenie und Klassifikation der sozialen Vespiden. *Zool. Jb. Abt. f. Syst.*, **36**: 303-330.
- EBERHARD, M. J. W. 1969. The social biology of polistine wasps. *Misc. Publs. Mus. Zool. Univ. Michigan*, No. 140, Ann Arbor, 101 pp., 23 figs.
- FIEBIGER, K. 1907. Eine Wespen zerstörende Ameise aus Paraguay. *Eciton vagans* Olivier. *Z. wiss. Insektbiol.*, **3**: 83-87.
- FLANDERS, S. E. 1945. Is caste differentiation in ants a function of the rate of egg deposition? *Science*, **101**: 245-246.
- . 1946. Control of sex and sex-limited polymorphism in the Hymenoptera. *Q. Rev. Biol.*, **21**: 135-143.
- . 1970. Cannibalistic infanticide in social Hymenoptera related to adult caste ratios. *Can. Ent.*, **102**: 898-905.
- GERVET, J. 1964a. Le comportement d'oophagie différentielle chez *Polistes gallicus* L. (Hymén., Vesp.). *Insectes Soc.*, **11**(4): 343-382.
- . 1964b. La ponte et sa régulation dans la société polygyne de *Polistes gallicus* L. (Hyménoptère, Vespide). *Annls Sci. nat., Zool.* 12^e Serie, **6**: 601-778.
- HAMAHER, J. I. 1936. Summer tanager (*Piranga rubra*) eating wasps. *Auk*, **53**: 220-221.
- HAMILTON, W. D. 1964a. The genetical evolution of social behaviour. I. *J. theor. Biol.*, **7**: 1-16.
- . 1964b. The genetical evolution of social behaviour. II. *J. theor. Biol.*, **7**: 17-52.

- HEIDMANN, G. 1936. Über das Leben auf Waben mit mehreren überwinterten Weibchen von *Polistes gallica* L. Biol. Zbl., **56**: 389-400.
- IHERING, H. VON. 1896. Zur Biologie der sozialen Wespen Brasiliens. Zool. Anz., **19**: 449-453.
- ISELY, D. 1922. Notes on nesting of *Polistes* (Hymenoptera, Vespidae). Kans. Univ. Sci. Bull., **14**(12): 341-343.
- ISHAY, J., H. BYTINSKI-SALZ, AND A. SHULOV. 1967. Contributions to the bionomics of the oriental hornet (*Vespa orientalis* Fab.). Israel J. Ent., **2**: 45-106.
- ISHAY, J., AND R. IKAN. 1968a. Gluconeogenesis in the oriental hornet *Vespa orientalis* F. Ecology, **49**(1): 169-171.
- . 1968b. Food exchange between adults and larvae in *Vespa orientalis* F. Anim. Behav., **16**(2-3): 298-303.
- JANET, C. 1903. Observations sur les guêpes. Paris, C. Naud. 85 pp.
- JEANNE, R. L. 1970a. Chemical defense of brood by a social wasp. Science, **168**: 1465-1466.
- . 1970b. Note on a bat (*Phylloderma stenops*) preying upon the brood of a social wasp. J. Mammal., **51**(3): 624-625.
- LÖVGREN, B. 1958. A mathematical treatment of the development of colonies of different kinds of social wasps. Bull. math. Biophys., **20**: 119-148.
- MASCHWITZ, U. 1966a. Larven als Nahrungsspeicher im Wespenvolk. Ein Beitrag zum Trophallaxisproblem. Verh. dt. zool. Ges. Jena 1965. Zool. Anz., **29**, Suppl.: 530-534.
- . 1966b. Das Speichelsekret der Wespenlarven und seine biologische Bedeutung. Z. vergl. Physiol., **53**: 228-252.
- MICHENER, C. D. 1964. Reproductive efficiency in relation to colony size in hymenopterous societies. Insectes Soc., **11**(4): 317-342.
- MORIMOTO, R. 1954a. On the nest development of *Polistes chinensis antennalis* Percz. I. (Studies on the social Hymenoptera of Japan. III). Sci. Bull. Fac. Agric. Kyushu Univ., **14**: 337-353.
- . 1954b. On the nest development of *Polistes chinensis antennalis* Perez. II. (Studies on the social Hymenoptera of Japan. IV). Sci. Bull. Fac. Agric. Kyushu Univ., **14**: 511-522.
- . 1954c. On the nest development of *Polistes chinensis antennalis* Perez. III. Relation between the removal of eggs and larvae from the nest and the oviposition of the founding female. (Studies on the social Hymenoptera of Japan. V). Sci. Bull. Fac. Agric. Kyushu Univ., **14**: 523-533.
- . 1960. Experimental study on the trophallactic behavior in *Polistes* (Hym., Vesp.). Acta hymenopt. Fukuoka, **1**(2): 99-103.
- . 1961a. On the dominance order in *Polistes* wasps I. (Studies on the social Hymenoptera in Japan. XII). Sci. Bull. Fac. Agric. Kyushu Univ., **18**(4): 339-351.
- . 1961b. On the dominance order in *Polistes* wasps II. (Studies on the social Hymenoptera of Japan. XIII). Sci. Bull. Fac. Agric. Kyushu Univ., **19**(1): 1-17.
- MYERS, J. G. 1929. The nesting together of birds, wasps, and ants. Proc. ent. Soc. London, **4**: 80-90.
- PARDI, L. 1940. Ricerche sui Polistini. I. Poliginia vera e apparente in *Polistes gallicus* (L.). Atti Soc. tosc. Sci. Nat. Pisa, **49**(4): 3-9.
- . 1942. Ricerche sui Polistini. V. La poliginia iniziale di *Polistes gallicus* (L.). Boll. Ist. Ent. Univ. Bologna, **14**: 1-106.
- . 1946. Ricerche sui Polistini. VII. La "dominazione" e il ciclo ovarico annuale in *Polistes gallicus* (L.). Boll. Ist. Ent. Univ. Bologna, **15**: 25-84.
- . 1947. Beobachtungen über das interindividuelle Verhalten bei *Polistes gallicus* (Untersuchungen über die Polistini, No. 10). Behaviour, **1**: 138-172.
- . 1948a. Ricerche sui Polistini. XI. Sulla durata della permanenza delle femmine nel nido e sull'accrescimento della società in *Polistes gallicus* (L.). Atti Soc. tosc. Sci. Nat. Pisa, **55**(B): 3-15.
- . 1948b. Dominance order in *Polistes* wasps. Physiol. Zool., **21**(1): 1-13.
- . 1951. Ricerche sui Polistini. XII. Studio della attività e della divisione di lavoro in una società di *Polistes gallicus* (L.) dopo la comparsa delle operaie. Arch. zool. ital., **36**: 363-431.
- PARDI, L., AND M. CAVALCANTI. 1951. Esperienze sul meccanismo della monoginia funzionale in *Polistes gallicus* (L.) (Hymenopt. Vesp.). Boll. Zool., **18**: 247-252.
- RAU, P. 1928a. The honey-gathering habits of *Polistes* wasps. Biol. Bull. mar. biol. Lab., Woods Hole, **54**: 503-519.
- . 1928b. Trophallaxis in *Polistes pallipes*. Psyche, Cambridge, **35**: 153-156.
- . 1930. Ecological and behavior notes on *Polistes pallipes*. Can. Ent., **62**: 143-147.
- . 1933. The jungle bees and wasps of Barro Colorado Island (with notes on other insects). Phil. Rau, Kirkwood, Mo., 324 pp.
- . 1938. Studies in the ecology and behavior of *Polistes* wasps. Bull. Brooklyn ent. Soc., **33**(5): 224-235.
- . 1939. Studies in the ecology and behavior of *Polistes* wasps. Bull. Brooklyn ent. Soc., **34**(1): 36-44.

- . 1940. The nesting habits of several species of Mexican social wasps. *Ann. ent. Soc. Am.*, **33**(1): 81–93.
- . 1941a. Observations on certain lepidopterous and hymenopterous parasites of *Polistes* wasps. *Ann. ent. Soc. Am.*, **34**: 355–366.
- . 1941b. Birds as enemies of *Polistes* wasps. *Can. Ent.*, **73**: 196.
- REED, W. W. 1941. The climates of the world. U. S. Dep. Agr. Yearbook, 1941: 665–684.
- REID, J. A. 1942. On the classification of the larvae of the Vespidae (Hymenoptera). *Trans. R. ent. Soc. London*, **92**: 285–331.
- RICHARDS, O. W. 1945. A revision of the genus *Mischocyttarus* de Saussure. *Trans. R. ent. Soc. London*, **95**: 295–462.
- . 1962. A revisional study of the masarid wasps (Hym., Vesp.). British Museum (N. H.), London, 294 pp.
- RICHARDS, O. W., AND M. J. RICHARDS. 1951. Observations on the social wasps of South America (Hymenoptera, Vespidae). *Trans. R. ent. Soc. London*, **102**: 1–170.
- RODRIGUES, V. M. 1968. Estudo sobre vespas sociais do Brasil (Hymenoptera, Vespidae). Doctoral Dissertation, Faculdade de Filosofia, Ciências e Letras de Rio Claro, Universidade de Campinas, Brasil, 113 pp.
- ROUBAUD, E. 1916. Recherches biologiques sur les guêpes solitaires et sociales d'Afrique. La genèse de la vie sociale et l'évolution de l'instinct maternal chez les Vespides. *Annls Sci. nat. Zool.*, 10^e Série, **1**: 1–160.
- SAKAGAMI, SH. F., AND H. FUKUDA. 1968. Life tables for worker honeybees. *Res. Popul. Ecol.*, **10**: 127–139.
- SALT, G., AND J. BEQUAERT. 1929. Stylopized Vespidae. *Psyche*, Cambridge, **36**: 249–282.
- SCHWARZ, H. F. 1929. Honey wasps. *Natur. Hist.*, New York, **29**(4): 421–426.
- . 1931. The nest habits of the diplopterous wasp *Polybia occidentalis* variety *scutellaris* (White) as observed at Barro Colorado, Canal Zone. *Am. Mus. Novitates*, No. 471: 1–27.
- SLOBODKIN, L. B. 1961. Growth and regulation of animal populations. New York, Holt, Rinehart and Winston, viii + 184 pp.
- SNELLING, R. R. 1953. Notes on the hibernation and nesting of the wasp *Mischocyttarus flavitarsis* (de Saussure) (Hym., Vesp.). *J. Kans. ent. Soc.*, **26**: 143–145.
- SWEZEY, O. 1910. The feeding habits of Hawaiian Lepidoptera. *Proc. Hawaii. ent. Soc.*, **2**(3): 131–193.
- TURNER, C. H. 1912. An orphan colony of *Polistes pallipes* Lepel. *Psyche*, Cambridge, **19**: 184–190.
- VECHT, J. VAN DER. 1966. The geographical distribution of the social wasps (Hymenoptera, Vespidae). *Proc. 12th Int. Congr. ent. London*, 1964(1965): 440–441.
- . 1968. The terminal gastral sternite of female and worker social wasps (Hymenoptera, Vespidae). *Proc. K. ned. Akad. Wet., Sect. C*, **71**(1): 411–422.
- VESEY-FITZGERALD, D. 1938. Social wasps (Hym. Vespidae) from Trinidad, with a note on the genus *Trypoxylon* Latreille. *Trans. R. ent. Soc. London*, **87**: 181–191.
- WEST, M. J. 1967. Foundress associations in polistine wasps: dominance hierarchies and the evolution of social behavior. *Science*, **157**: 1584–1585.
- WHEELER, W. M. 1925. The finding of the queen of the army ant *Eciton hamatum* Fabricius. *Biol. Bull. mar. biol. Lab.*, Woods Hole, **49**: 139–149.
- WILLIAMS, F. X. 1928. Studies in tropical wasps—their hosts and associates (with descriptions of new species). *Bull. Exp. Stn Hawaii. Sug. Plrs Assoc., Ent. Ser.* No. 19, 179 pp.
- WILLINK, A. 1953. Las especies argentinas de *Mischocyttarus* de Saussure (Hym. Vespidae). *Acta zool. Lilloana*, **14**: 317–340.
- WILSON, E. O. 1953. On Flanders' hypothesis of caste determination in ants. *Psyche*, Cambridge, **60**: 15–20.
- YOSHIKAWA, K. 1955. A polistine colony usurped by a foreign queen. *Ecological studies of Polistes wasps*, II. *Insectes Soc.*, **2**(3): 255–260.
- . 1962. Introductory studies on the life economy of polistine wasps. I. Scope of problems and consideration on the solitary stage. *Bull. Osaka Mus. nat. Hist.*, **15**: 3–27.
- . 1963a. Introductory studies on the life economy of polistine wasps. II. Superindividual stage. 3. Dominance order and territory. *J. Biol. Osaka Cy Univ.*, **14**: 55–61.
- . 1963b. Introductory studies on the life economy of polistine wasps. III. Social stage. *J. Biol. Osaka Cy Univ.*, **14**: 63–66.
- ZIKÁN, J. F. 1935. Die sozialen Wespen der Gattung *Mischocyttarus* Sauss., nebst Beschreibung von 27 neuen Arten (Hym., Vespidae). *Archos. Inst. Biol. veg.*, Rio de Janeiro, **1**: 143–203.
- . 1949. O gênero *Mischocyttarus* Saussure (Hym., Vespidae), com a descrição de 82 espécies novas. *Parque Nacional do Itatiaia, Bol. Nr.* 1: 1–251.
- . 1951. Polymorphismus und Ethologie der sozialen Faltenwespen (Vespidae, Diploptera). *Acta zool. Lilloana*, **11**: 5–51.



Plate 1. Fig. 1. Study site, Belém. The area is poorly drained, with a cover of tall grass and occasional clumps of low trees. Nests of *M. drewseni* were found under the eaves and window lintels of the house just to the left of the center of the picture. Fig. 2. Study site, Taperinha. In the foreground is "terra firme," covered in grass and other low vegetation. *M. drewseni* foraged here, and for short distances out over the varzea vegetation of the middle ground. At the time the picture was taken (May), the varzea was submerged by the annual flooding of the Amazon. The bush in the lower righthand corner of the picture was the site of nest 349.



Plate II. Fig. 3. Nesting sites, Taperinha. Nests of *M. drewseni* were common under the edge of the gallery (just above the top of the ladder). Fig. 4. Nesting sites, Taperinha. *M. drewseni* nested on the meteorological shacks in the foreground, under the tiles stacked behind the shacks, and under the eaves of the house in the background.



Plate III. Fig. 5. Postemergence nest of *M. drewseni*, side view. About $1\frac{1}{2}$ times natural size. Fig. 6. Postemergence nest of *M. drewseni* from below, showing the nest face. The light-colored pupal cap to the lower right of the center of the nest was recently spun by the larva and has not yet had pulp applied to it. Larvae are visible in some of the open cells. Slightly larger than natural size.

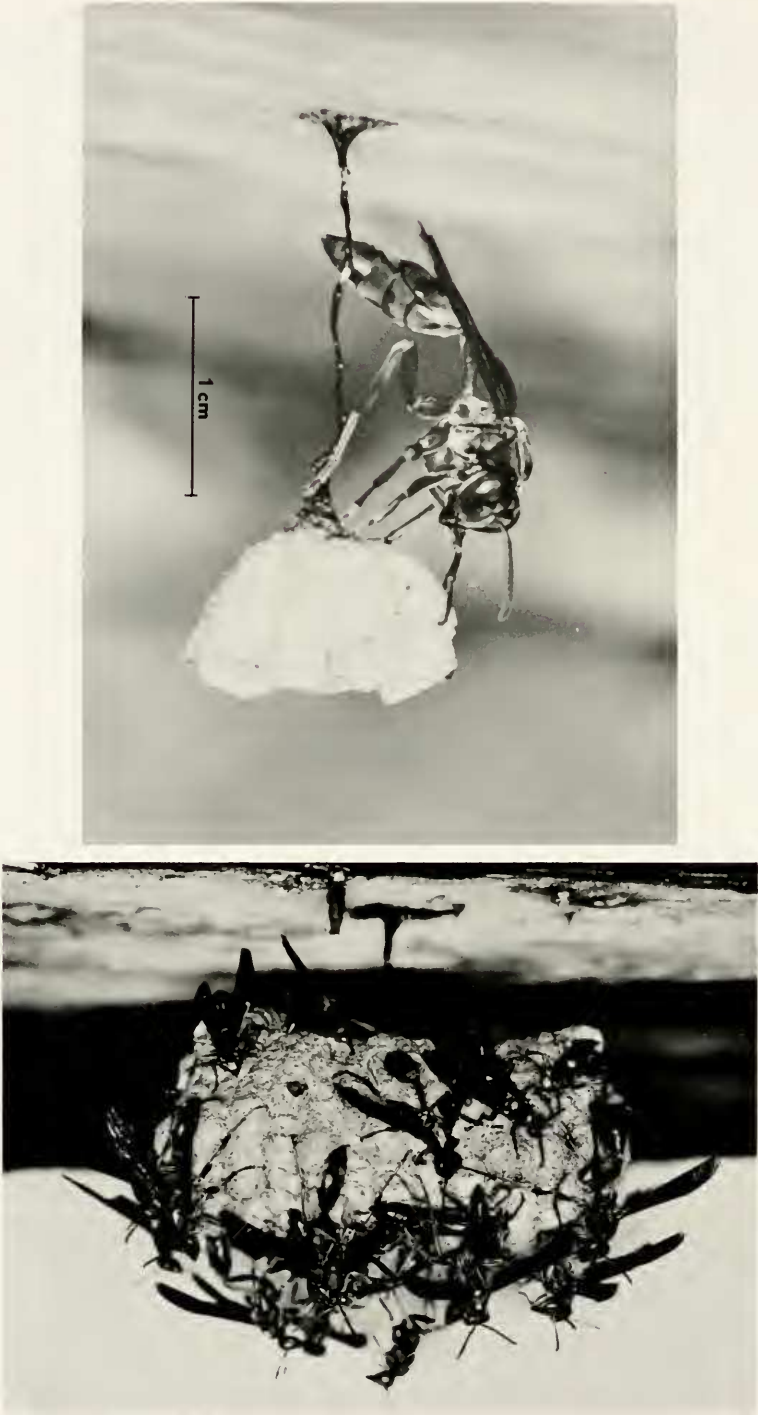


Plate IV. Fig. 7. A female applying the ant repellent secretion by rubbing the tuft of hair on the terminal gastral sternite against the surface of the nest stem (from Jeanne, 1970a). Fig. 8. Alarm response to movement of a large object below the nest. The wasps have spread their wings and are facing the disturbance.